A process-based model for methane emission predictions from flooded rice paddies.

van Bodegom, P.M.; Wassmann, R.; Metra-Corton, T.M.

published in
Global Biogeochemical Cycles
2001

DOI (link to publisher)
10.1029/1999GB001222

document version
Publisher's PDF, also known as Version of record

GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 15, NO. 1, PAGES 247–263, MARCH, 2001

A process-based model for methane emission predictions from flooded rice paddies

P. M. van Bodegom[1]
Laboratory of Microbiology, Wageningen University and Research Center (WUR), Wageningen, Netherlands

R. Wassmann
Soil and Water Sciences Division, International Rice Research Institute, Los Baños, Philippines

T. M. Metra-Corton
Agronomy, Soils and Plant Physiology Division, Philippine Rice Research Institute, Muñoz, Nueva Ecija, Philippines

Abstract. Estimation and prediction of methane emission from flooded rice paddies is impaired by the large spatial and temporal variability in methane emissions and by the dynamic nonlinear relations between processes underlying methane emissions. This paper describes a process-based model on methane emission prediction from flooded rice paddies that can be used for extrapolation. The model is divided into two compartments; rhizosphere, which is a function of root length density, and bulk soil. The production of carbon substrates drives methane emission and originates from soil organic matter mineralization, organic fertilizer decomposition, in both compartments, and root exudation and root decay, in the rhizosphere compartment only. It is assumed that the methanogens are completely outcompeted for acetate by nitrate and iron reducers but that competition takes place with sulfate reducers. Produced methane is transported to the root surface in the rhizosphere or the soil-water interface in the bulk soil. Transport time coefficients are different for the two compartments. Part of the methane is oxidized, a constant fraction of produced methane in the bulk soil, whereas the oxidation fraction varies according to root activity dynamics in the rhizosphere. The remaining methane is emitted to the atmosphere. The model was validated with independent field measurements of methane emissions at sites in the Philippines, China, and Indonesia with only few generally available site-specific input parameters. The model properly predicts methane emission dynamics and total seasonal methane emission for the sites in different seasons and under different inorganic and organic fertilizer conditions. A sensitivity analysis on model assumptions showed that the assumptions made in this model are reasonable and that the division into two compartments was necessary to obtain good results with this model. The combination of proper prediction and the necessity of few input parameters allow model application at regional and global scales.

1. Introduction

Methane is one of the principal greenhouse gases, and rice paddy fields are among the most important sources of atmospheric methane [*Houghton et al.*, 1996]. Precise estimates of global methane emissions from rice paddies are, however, not available and depend on the approaches, techniques, and databases used. One principal cause for uncertainties in global estimates results from the large, intrinsic spatial and temporal variability in methane emissions. This variation in methane emissions is only partly explained by correlations with environmental variables [*Walter et al.*, 1996]. This is attributed to the diurnal and seasonal dynamic and nonlinear interactions between processes underlying methane emissions. A process-based model, quantifying the functional relationships between methane emissions and the most important underlying processes, methane production, oxidation, and transport, may improve insight in these relations and may thus contribute to a reduction of the uncertainties in global methane emission estimates from rice paddies. This paper presents a process-based model that predicts seasonal methane emissions from flooded rice fields that can be applied at large scales using Geographic Information System (GIS). Such a model must be simple, by lack of mechanistic knowledge, balanced, and process-based to cope with encountered variability and to avoid site-specific calibrations. In addition, such a model should use only a few site characteristics as input parameters to avoid an excessively high data demand for the GIS and to allow scenario analyses at a larger spatial and temporal scale.

For this particular objective, other models on methane emissions from wetlands, including rice paddies, developed for different objectives and with different degrees of mechanistic detail, seem less suitable. Some models use methane emission data to parameterize empirical relations for some of the underlying processes [*Hosono and Nouchi*, 1997; *Huang et al.*, 1998], which may be problematic for extrapolation to larger scales owing to the nonlinear interactions and the number of fitted parameters. Some more process-based models [*Arah and Stephen*, 1998; *Walter et al.*,

[1]Also at Department of Theoretical Production Ecology (WUR), Wageningen University and Research Center, Wageningen, Netherlands.

Paper number 1999GB001222.
0886-6236/01/1999GB001222$12.00

1996] describe all processes as mechanistically as possible, although mechanistic knowledge on the spatial characteristics of driving variables, especially for methane production and gas transport, is scarce. Some parameters therefore have to be calibrated for each site specifically, particularly on methane production potential and plant transport characteristics. This necessary calibration limits the extrapolation possibilities of the models. Other process-based models emphasize methane production, whereas the descriptions of methane oxidation and methane transport are highly simplified [*Cao et al.*, 1995; *James*, 1993].

The processes leading to methane emissions are highly different for the rhizosphere and the remaining part of the soil, the bulk soil (see section 2.1). In our model, the soil is therefore divided into two compartments, a rhizosphere and a bulk soil, without considering soil layers. This distinction allows an efficient and well-balanced approach for constructing a simple process-based model because use can be made of the process differences between each compartment. With these two compartments, the variability can be decreased more efficiently than with a soil layer model because differences between soil layers are smaller than differences between rhizosphere and bulk soil. The model was validated against independent experimental data collected by an automatic measurement system based on the closed chamber technique [*Wassmann et al.*, 1994] in flooded rice fields at two sites in the Philippines, one site in China, and one site in Indonesia, while using only generally available site-specific parameters. A sensitivity analysis of the model was carried out to evaluate the assumptions made in the model. This sensitivity analysis was also helpful in obtaining insight in important gaps of knowledge.

2. Model Description

2.1. Two Model Compartments: Bulk Soil and Rhizosphere

Methane emissions from rice fields are strongly influenced by the presence of the rice plants. Methane emissions are higher with rice plants than without [*Holzapfel-Pschorn et al.*, 1986], and methane emissions are dominated by plant-mediated emissions [*Schütz et al.*, 1989b]. Recognition of the importance of rice plants has led to the development of correlative models between methane emissions and plant parameters [e.g., *Sass et al.*, 1990; *Watanabe et al.*, 1994], although such correlations could not always be found [e.g., *Denier van der Gon and Neue*, 1996; *Watanabe et al.*, 1995]. For a better quantitative understanding of the rice plant influence, the various processes by which the plant modifies methane emissions must be considered. The model quantifies these different processes of plant influence in a separate compartment, the rhizosphere. All other processes leading to methane emissions occur in a bulk soil compartment. The processes occur independently in both compartments outlined in Figure 1 and differ in some characteristics for the compartments: Organic matter in the rhizosphere is not only released by soil mineralization and straw and stubble decomposition but also by root exudation and root decay. Methane is transported by plant-mediated transport in the rhizosphere, while ebullition and diffusion are the major transport routes in the bulk soil. The oxygen used for methane oxidation in the rhizosphere comes from root oxygen release (ROL), whereas oxygen enters the bulk soil by diffusion through the soil-water interface. Before describing these processes in more detail, the distribution of the soil between the compartments during the season is treated.

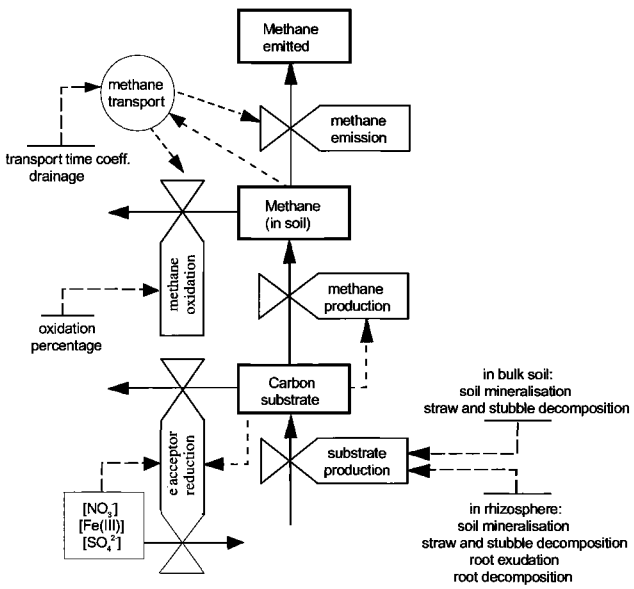


Figure 1. Relational diagram of the flow of carbon for each compartment in the model.

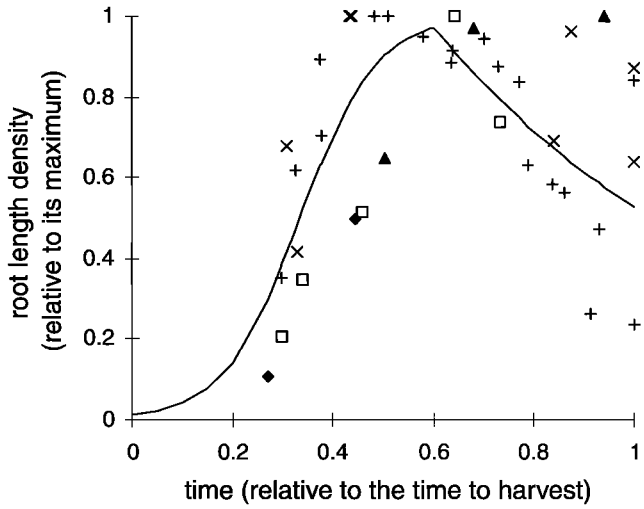


Figure 2. Time course of the relative root length density during the growth of the rice crop as derived from literature (crosses [*Beyrouty et al.*, 1988], filled diamonds [*Drenth et al.*, 1991], filled triangles [Kang et al., 1995], pluses [*Slaton et al.*, 1990], open squares [*Teo et al.*, 1995]). Time is taken relative to the time of harvest. If there are no data on the length of the season, the length of the growing season is estimated from data on climate and cultivar.

The rice crop influences the processes underlying methane emissions via its roots. In general, the uptake and release of solutes and gases depend on the root length density (RLD) [*Armstrong and Beckett*, 1987; *Kirk and Solivas*, 1997]. RLD is empirically related to its maximum root length density (RLD_{max}) based on data by *Beyrouty et al.* [1988], *Drenth et al.* [1991], *Kang et al.* [1994], *Slaton et al.* [1990], and *Teo et al.* [1995] and fitted by minimizing the mean square error (MSE) to a cumulative logistic growth curve up to RLD_{max} and an exponential decrease after RLD_{max} (Figure 2) as from that moment on roots start to decay:

$$RLD = \frac{RLD_{max}}{1 + Ke^{-rgr(time')}} \qquad RLD < RLD_{max}$$

$$RLD = \frac{RLD_{max}}{1 + Ke^{-rgr(time')_{mor}}} e^{-k_{mor}(time' - time'_{mor})} \qquad RLD \geq RLD_{max}, \tag{1}$$

Table 1. General Process Model Parameters Kept Constant at All Conditions

Parameter	Description	Value	Unit
K	relative rice biomass increase	85.5	
rgr	rice relative growth rate	13.3	
k_{mor}	relative root mortality rate	1.30×10^{-7}	s^{-1}
$time'_{mor}$	relative time of mortality start	0.6	
R_{min}	initial soil mineralization parameter	1.25×10^{-4}	$s^{-0.415}$
S_{min}	relative soil mineralization decrease	0.585	
Q_{10}	temperature correction factor	2.85	
R_{fert}	initial straw decomposition parameter	5.77×10^{-2}	$s^{-0.623}$
S_{fert}	relative straw decomposition decrease	0.377	
B_{exu}	baseline root exudation rate	0.85×10^{-6}	mol m^{-3} s^{-1}
A_{exu}	maximum root exudation rate increase	4.41×10^{-6}	mol m^{-3} s^{-1}
$time'_{max}$	moment of maximum root exudation	0.552	
σ	relative rate of root exudation change	0.14	
$K_{d,root}$	root decomposition constant	6.5×10^{-8}	s^{-1}
k_{reox}	relative reoxidation rate	e^-acc dep.	s^{-1}
$\tau_{rhizosphere}$	rhizosphere transport time coefficient	9×10^3	s
τ_{bulk}	bulk soil transport time coefficient	1.08×10^6	s
B_{oxi}	baseline methane oxidation	0.10	
A_{oxi}	maximum methane oxidation increase	0.63	

in which $time'$ is the relative time (time divided by the total length of the plant growing season) and rgr (relative growth rate), K $[(RLD_{max}\text{-}RLD_{t=0})/RLD_{t=0}]$, k_{mor} (relative root mortality rate), and $time_{mor}'$ (relative time at which roots start to die) are dimensionless empirical parameters (Table 1).

At good crop performance and at normal plant densities, almost all methane is emitted via the plant around RLD_{max} [*Schütz et al.*, 1989b; *Wassmann et al.*, 1996]. It can thus be assumed that the fraction of the soil under influence of the rhizosphere compartment (F_rhizosphere) is a function of RLD_{max}:

$$F\_\text{rhizosphere} = \frac{\text{RLD}}{\text{RLD}_{max}}. \quad (2)$$

With a change in RLD during the season, the contribution of the rhizosphere compartment changes. F_rhizosphere is zero in absence of plants, i.e., before transplanting. The fraction of the bulk soil is one minus F_rhizosphere. The model is not subdivided into different soil layers, as initial soil conditions are constant throughout the soil up to the rooting depth by puddling. Heterogeneities with depth formed during the season under influence of the rice plant are accounted for by the development of the rhizosphere compartment. All compounds are expressed in local within-compartment concentrations and are thus not affected by such heterogeneities. Methane transport rates may be affected by the use of depth-averaged parameter values. This has no large implications as the model is not sensitive to the value of transport parameters [*van Bodegom et al.*, 2000].

2.2. Carbon Substrate Production

Methane emissions are driven by the production of a carbon substrate, mainly acetate, CO_2/H_2, and formate (in mol C m^{-3} s^{-1}), for methane production. Carbon substrates are produced by anaerobic soil organic matter mineralization and decomposition of added organic material (in both compartments) and by root exudation and root decay (in the rhizosphere compartment only). These production rates need to be modeled explicitly to allow the prediction of methane emissions. It is assumed that carbon substrates are converted in the same compartment as they are produced. This seems reasonable as the turnover time of CO_2/H_2 and probably for formate as well is around 1 min [*Conrad et al.*, 1989a, 1989b]. The turnover time of acetate, and thus the possibilities for transport and exchange between compartments, is larger. In absence of plants and at the start of the season, when methane production and the rhizosphere compartment are very small, turnover times of acetate are 10–16 hours [*Krumböck and Conrad*, 1991; *Schütz et al.*, 1989a; *Sigren et al.*, 1997], which is equivalent to a maximum diffusion distance of ~7.5 mm. When methane production is important and when exchange may occur, i.e., while the rhizosphere compartment is well developed, turnover times of acetate are less than 1.5 hours, with a maximum diffusion distance of 2 mm [*Sigren et al.*, 1997].

Anaerobic soil organic matter mineralization releases small organic compounds by the breakdown of soil organic matter. Soil mineralization rates are not constant but decrease during the season owing to a decrease in easily accessible organic material. This can be taken into account by the use of a multicomponent model in which organic substrates are partitioned into several components according to their resistance to mineralization. Each component follows first-order kinetics but with a different relative decomposition coefficient [e.g., *Jenkinson et al.*, 1992; *Parton et al.*, 1987]. The principal problem with such models is that the quantities of the individual components cannot be determined directly by analytical fractionation procedures [*Paustian et al.*, 1992]. As a consequence, the components have to be reconstructed indirectly by fitting. An alternative approach is to define one pool of substrates but decrease its relative mineralization rate over time [*Yang*, 1996]. The 2nd approach needs fewer parameters to describe mineralization, P_{min} (in mol C m^{-3} s^{-1}) and is independent of whether the systems are aerobic or anaerobic. This approach was therefore used as default in this study and leads to the following [*Yang*, 1996]:

$$P_{min} = C_{min}(1 - S_{min})\, K_{d_{min}} e^{-K_{d_{min}}(\text{time})} \quad (3)$$

in which C_{min} is the soil organic carbon pool (mol C m^{-3}) and

$$K_{d_{min}} = R_{min}\, time^{-S_{min}}. \quad (4)$$

R_{min} ($S^{S_{min}-1}$) and S_{min}(−) are parameters that have to be determined experimentally. Temperature influence on mineralization rates is described using a Q_{10} value, defined as the relative increase in reaction rates at a temperature increase of 10°C:

$$P_{minT} = P_{minT_{ref}}\, Q_{10}^{\frac{T-T_{ref}}{10}}. \quad (5)$$

The reference temperature (T_{ref}) in this study is 30°C. For a rice soil the R_{min}, S_{min} and Q_{10} are taken from soil incubation studies [*van Bodegom and Stams*, 1999] by minimizing MSE (Table 1). Measured and calculated mineralization rates at different tempera-

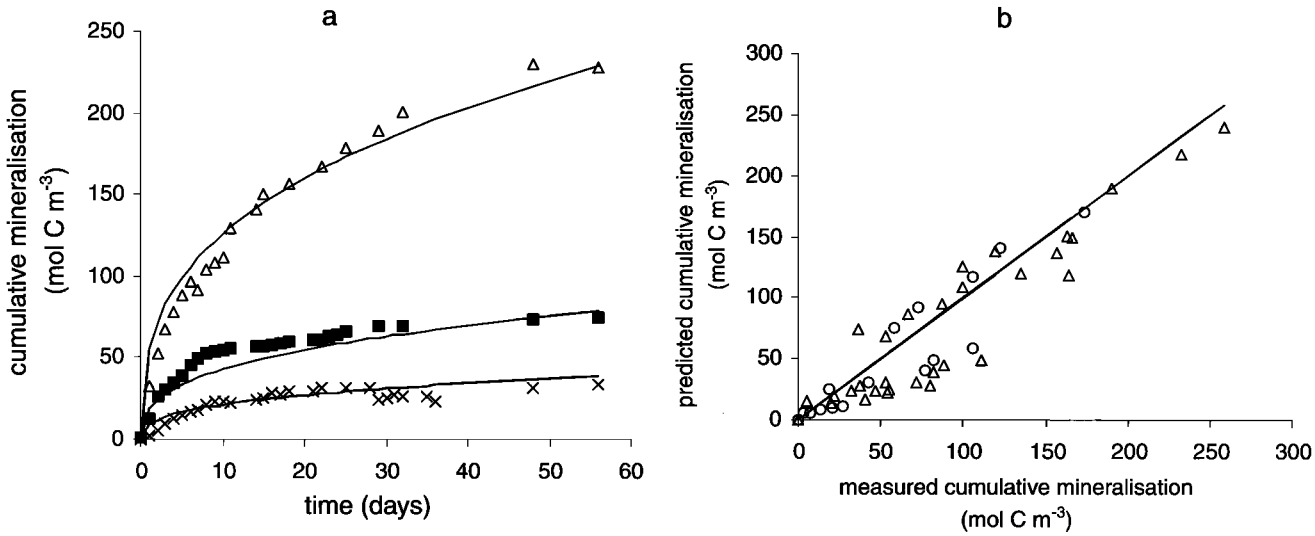


Figure 3. (a) Calibrated (based on equations (3)–(5)) (lines) and measured cumulative mineralization in an incubation study with rice paddy soil at 14°C (crosses), 20°C (filled squares), and 30°C (open triangles). (b) Validation of the calibrated mineralization model with independent data presented by *Tsutsuki and Ponnamperuma* [1987] (triangles) and *Inubushi et al.* [1997] (circles).

tures are depicted in Figure 3a. The same empirical parameter values can describe anaerobic soil mineralization rates in rice paddy soils presented by *Tsutsuki and Ponnamperuma* [1987] and *Inubushi et al.* [1997] (Figure 3b). It is therefore concluded that this description may be applied to rice paddy soils in general.

Organic fertilizers are sometimes added as extra substrates in rice paddies. The most common organic fertilizers are green manure and rice straw. Organic material from the previous crop, stubble and dead roots, is an additional source of organic material. The decomposition of such compounds, P_{fert} (in mol C m^{-3} s^{-1}) is usually described as a first-order decomposition rate:

$$P_{\text{fert}} = C_{\text{fert}} K_{d_{\text{fert}}} e^{-K_{d_{\text{fert}}}(\text{time}-t\_\text{added})} \quad (6)$$

in which C_{fert} (mol C m^{-3}) is the organic fertilizer applied at time t_added (s) and $K_{d,\text{fert}}$ (s^{-1}) the relative decomposition rate is considered as a constant. Analysis of data on $K_{d,\text{fert}}$ for rice straw [*Acharya*, 1935; *Murthy et al.*, 1991; *Neue and Scharpenseel*, 1987; *Saini*, 1989; *Singh et al.*, 1992; *Watanabe*, 1984; *Watanabe et al.*, 1998] shows, however, a clear relationship between incubation period and $K_{d,\text{fert}}$ (Figure 4). The decomposability of organic material changes with time. To account for this change, the decomposition rate of organic fertilizers is described similarly to the soil mineralization rate with R_{fert} and S_{fert} instead of using (6):

$$P_{\text{fert}} = C_{\text{fert}}(1 - S_{\text{fert}}) K_{d_{\text{fert}}} e^{-K_{d_{\text{fert}}}(\text{time}-t\_\text{added})}$$

and

$$K_{d_{\text{fert}}} = R_{\text{fert}} \,\text{time}^{-S_{\text{fert}}}. \quad (7)$$

R_{fert} and S_{fert} were determined for rice straw by minimizing the MSE for the data in Figure 4 (Table 1). Other organic fertilizers will have different values for R_{fert} and S_{fert}. Organic fertilizer decomposition rate is assumed to have a Q_{10} of 2.

Root exudation is passive, and active release of carbon compounds from the rice roots into the soil. Root exudation changes during the season and is affected by environmental conditions. Mineral deficiencies [*Kludze and Delaune*, 1995] and low radiation intensity [*Butterbach-Bahl*, 1992] decrease root exudation, while root exudation increases under the influence of a low redox potential [*Sass and Fisher*, 1995] and drought stress [*Turner*, 1986] and in the presence of organic fertilizers [*Sass et al.*, 1991b]. However, quantitative information on these influences is scarce and therefore cannot be incorporated in the model. Only information on a well-growing cultivar IR72 [H. K. Kludze, personal communication, 1998; *Minoda and Kimura*, 1994; *Minoda et al.*, 1996; *Lu et al.*, 1999] is available to construct a Gaussian curve, by minimizing MSE that describes the change in root exudation rate P_{exu} (mol C m^{-3} s^{-1}) during the season (Figure 5):

$$P_{\text{exu}} = B_{\text{exu}} + A_{\text{exu}} \exp\{-0.5[(\text{time}' - \text{time}'_{\text{max}})/\sigma]^2\} \quad (8)$$

in which B_{exu} is the baseline root exudation rate at transplanting and A_{exu} is the maximum increase in root exudation rate. This

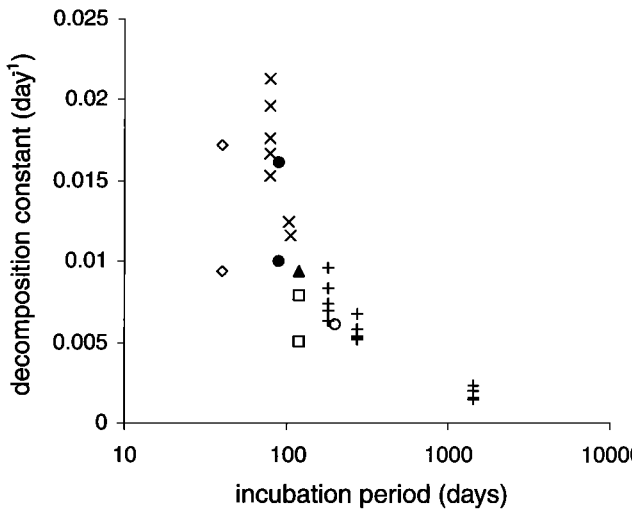


Figure 4. Decomposition constants for the decomposition of rice straw calculated from literature after different incubation periods (crosses [*Watanabe*, 1981], pluses [*Neue and Scharpenseel*, 1987], open diamonds [*Murthy et al.*, 1991], open squares [*Acharya*, 1935, filled triangles [*Watanabe et al.*, 1998], filled circles [*Singh et al.*, 1992], open circle [*Saini*, 1989]).

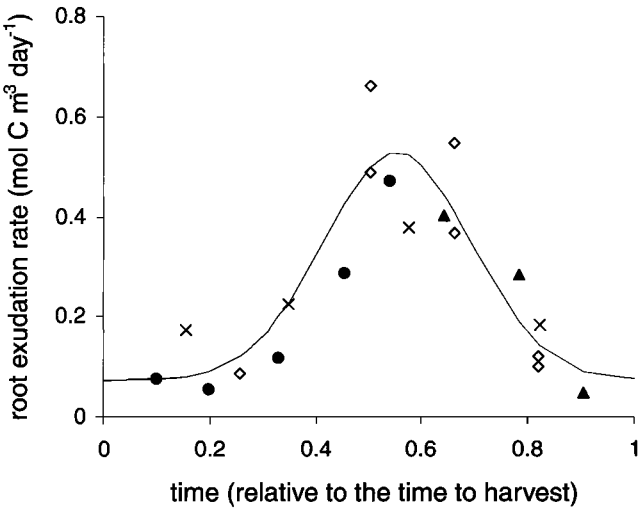


Figure 5. Fitted and measured root exudation rates from an IR72 rice cultivar at different moments during the growing season (crosses (H. K. Kludze, personal communication, 1998), open diamonds [*Minoda et al.*, 1996], filled triangles [*Minoda and Kimura*, 1994], filled circles [*Lu et al.*, 1999]).

maximum is obtained if the time′ = time_{max}′ and the relative rate of change to and from the maximum is expressed by σ (Table 1). This curve can thus describe the decrease in root activity after anthesis but may apply only to IR72. A change in the size of the rhizosphere compartment also influences the total amount of root exudation in the soil as root exudation rate is expressed per m^3.

Finally, organic substrates can be produced by rice root decay. This is mainly important at the end of the season, as can be seen from the change in the size of the rhizosphere compartment (Figure 2). As quantitative data are scarce, root mortality is determined from this curve as a first-order decay with k_{mor} as an exponent starting at time_{mor}′. Root decomposition (in mol C m^{-3} s^{-1}), releasing carbon substrates, is also approached by a first-order decay:

$$P_{root} = K_{d_{root}} (\text{pool of dead roots}). \quad (9)$$

$K_{d,root}$ is the decomposition constant for roots (Table 1), estimated from *Saini* [1989] and is assumed to have a Q_{10} of 2. Changes in the pool of dead roots (in mol m^{-3}) is equal to the difference between root mortality and root decomposition rates.

2.3. Methane Production

Some simplified models [e.g., *Cao et al.*, 1995] relate methane production to the redox potential (Eh) to avoid a difficult mechanistic description of methane production. There are several reasons not to choose the easily measurable parameter Eh as a determining parameter in this model: (1) Eh is the resultant of all kinds of compounds, which makes it difficult to investigate specific effects, for example, the addition of inorganic fertilizers or dynamic water tables in rain fed systems. (2) Eh is a spatially averaged value, not taking into account gradients of electron acceptors or other heterogeneities. (3) Methanogens, methane-producing bacteria, are able to modify Eh to generate a favorable environment [*Fetzer and Conrad*, 1993]. (4) The critical Eh value for methane production varies considerably from +150 to −200 mV [*Devai and Delaune*, 1996; *Masscheleyn et al.*, 1993; *Mayer and Conrad*, 1990, *Peters and Conrad*, 1995; *Wang et al.*, 1992, 1993] and seems to vary with the type of electron acceptors present in the soil. All these values are far below the threshold value of +420 mV given by *Fetzer and Conrad* [1993]. (5) Eh is hard to predict as *Ratering and Conrad* [1998] showed that concentration changes in iron(II) and especially in sulfate did not follow Eh changes.

Therefore an approach is chosen in which the underlying parameters and processes itself are used: It is assumed that all available substrate is consumed directly either by methanogens or by other anaerobic bacteria using alternative electron acceptors (all conversion rates in mol m^{-3} s^{-1}). No severe substrate accumulation occurs, which seems, based on experimental data [e.g., *Achtnich et al.*, 1995a; *Rothfuss and Conrad*, 1993], reasonable in periods that methane production is predominant.

Simulation time starts after flooding the soil and thus is oxygen absent in the bulk soil. Oxygen concentrations in the rhizosphere are low [*Gilbert and Frenzel*, 1995], and it is assumed that these concentrations are too low to inhibit methane production or to allow reoxidation of electron acceptors or aerobic respiration. It is assumed that all oxygen is consumed by methane oxidizers, which can operate at these low-oxygen concentrations because of their high affinity for oxygen [*Frenzel et al.*, 1990]. NO_3^- is thus the first electron acceptor to be reduced:

$$\frac{d[NO_3]}{d\text{time}} = -\nu_{NO_3} \sum P_x \quad (10a)$$

in which ν_{NO_3} is a stoichiometry factor for the carbon substrate needed to reduce NO_3^- and $\sum P_x = P_{min} + P_{fert}$ or $\sum P_x = P_{min} + P_{fert} + P_{exu} + P_{root}$ for the bulk soil and rhizosphere, respectively. After NO_3^-, Fe(III) is reduced,

$$\frac{d[\text{Fe(III)}]}{d\text{time}} = -\nu_{Fe} \sum P_x. \quad (10b)$$

Methanogens and sulfate reducers are outcompeted by nitrate reducers [*Achtnich et al.*, 1995b; *Westermann and Ahring*, 1987] and by iron reducers [*Lovley and Phillips*, 1986, 1987]. In addition, methane production is inhibited by accumulated NO and N_2O [*Klüber and Conrad*, 1998]. Methane production and sulfate reduction therefore start after NO_3^- and Fe(III) disappearance. Sulfate reducers outcompete methanogens for H_2/formate, but some competition is possible for acetate [*Achtnich et al.*, 1995b; *Westermann and Ahring*, 1987]. In addition, H_2S can inhibit methanogenic activity at high concentrations. All these interactions are summarized by

$$\frac{d[SO_4^{2-}]}{d\text{time}} = -\nu_{SO_4} \frac{[SO_4^{2-}]}{[SO_4^{2-}]_{t=0}} \sum P_x \quad (10c)$$

$$\frac{d[CH_4]}{d\text{time}} = \nu_{CH_4} \frac{[SO_4^{2-}]_{t=0} - [SO_4^{2-}]}{[SO_4^{2-}]_{t=0}} \times \sum P_x - \text{CH}_4\text{\_transport\_rate}. \quad (11a)$$

After all alternative electron acceptors have been reduced, all substrate is converted by methanogens:

$$\frac{d[CH_4]}{d\text{time}} = \nu_{CH_4} \sum P_x - \text{CH}_4\text{\_transport\_rate}. \quad (11b)$$

The CH_4_transport_rate is treated in section 2.4. Equations (10a–c) and (11a,b) are independent of the mechanism involved in the inhibition of methane production, whether it is by specific inhibition, by competition, or by a methanogenic biomass limitation at the start of the season. The model does not specifically incorporate pH effects, as soil pH changes are highly correlated to Eh changes [*Tsutsuki and Ponnamperuma*, 1987]. After alternative electron acceptor depletion, soils have a pH of around 7 [*Tsutsuki and Ponnamperuma*, 1987], at which methanogenesis is around its optimum value [*Minami*, 1989; *Wang et al.*, 1993]. Inhibiting effects by salinity are not treated either, as such effects happen under extreme conditions only [*Denier van der Gon and Neue*, 1995b].

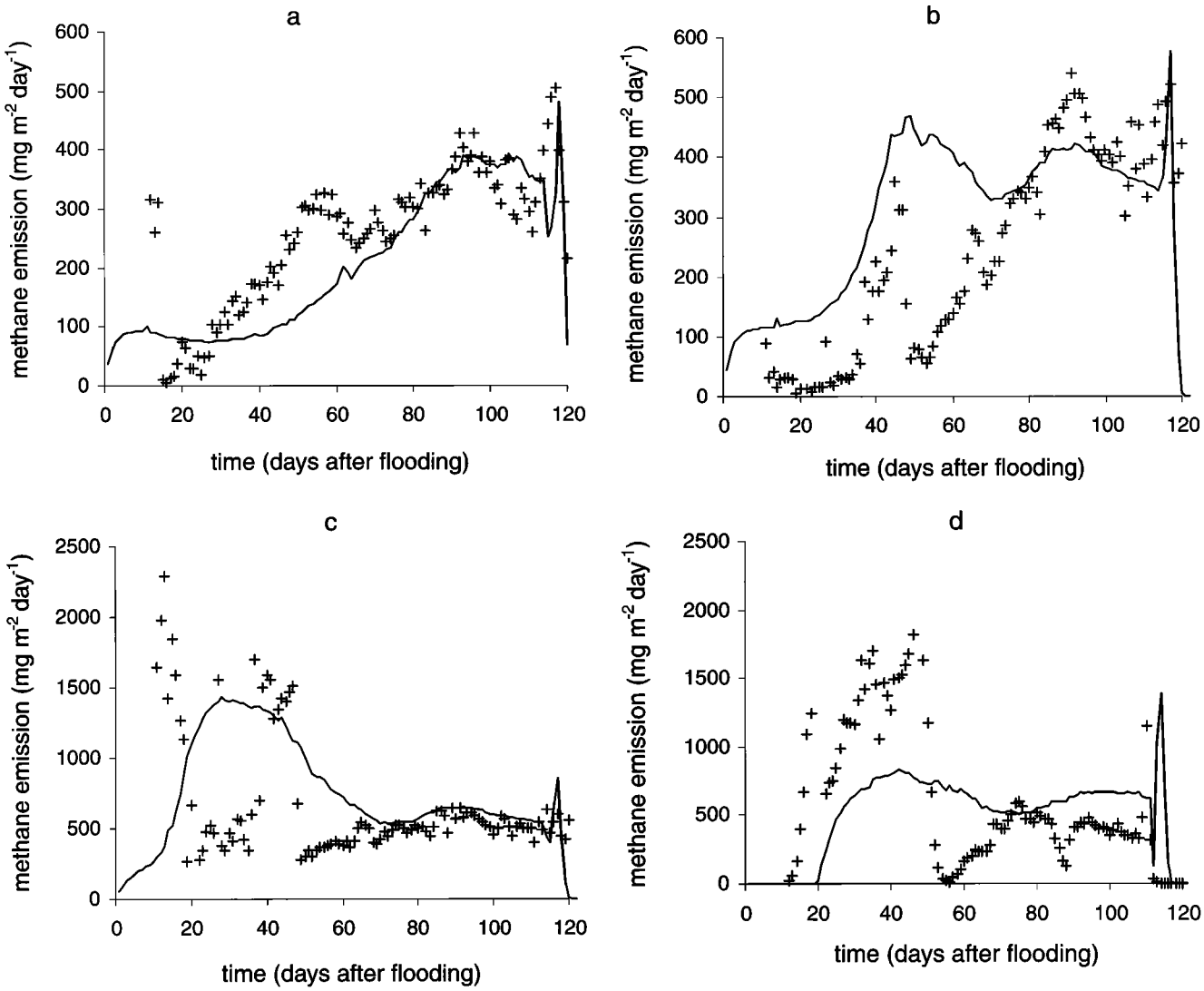


Figure 6. Model validation. Comparison of measured (pluses) and modeled (lines) methane emissions at different locations, with different seasons and treatments for (a) MA 94 control, (b) MA 96 control, (c) MA 96 with straw, (d) LB 97 with straw, (e) LB 97 control, (f) LB 97 with $(NH_4)_2SO_4$, (g) BG 97 control, (h) BG 97 with straw, and (i) JK 96 control. Note the different scales at the y axes. (j) Comparison of modeled seasonal methane emissions and measured seasonal methane emissions.

Under aerobic conditions, methane production stops and reduced electron acceptors (e^-acc_{red}) are reoxidized. Reoxidation rates (reoxi_rate) (in mol m^{-3} s^{-1}) of ferrous iron, sulphide, and FeS are described by first-order kinetics:

$$\text{reoxi\_rate} = k_{reox}[e^- acc_{red}] \quad (12)$$

in which k_{reox} is the relative reoxidation constant of 1.27 10^{-4} s^{-1}, 5.6 10^{-6} s^{-1}, and 7.6 10^{-7} s^{-1} for ferrous iron, sulphide, and FeS, respectively [*van Bodegom et al.*, 2000]. Other reoxidation processes are not treated for reasons given elsewhere [*van Bodegom et al.*, 2000].

2.4. Methane Transport

In the model, produced methane is transported to an anaerobic/aerobic interface; the root surface in the rhizosphere compartment or the soil-water interface in the bulk soil compartment. Different transport mechanisms of gases in rice paddies, plant-mediated transport, diffusion through the soil, and ebullition, to these interfaces are lumped into a transport time coefficient, τ, which is the average period (in seconds) between production and the moment of reaching the interface:

$$CH_4\text{\_transport\_rate} = \frac{[CH_4]}{\tau} \quad (13)$$

in which $[CH_4]$ is the methane concentration (in mol m^{-3}) in a compartment. Transport time coefficients depend on path length and diffusion coefficient, which are assumed to be constant under flooded conditions. The τ values differ for each compartment. Equation (13) implies that methane produced in one compartment cannot leave the system through another compartment. In reality, some methane produced in the bulk soil may, however, leave the system through the plant if the roots capture gas bubbles formed in the bulk soil. Diffusion calculations taking into account transport resistances indicate that methane transport from bulk soil to rhizosphere will be small (data not shown). Even if such exchange occurs, it will

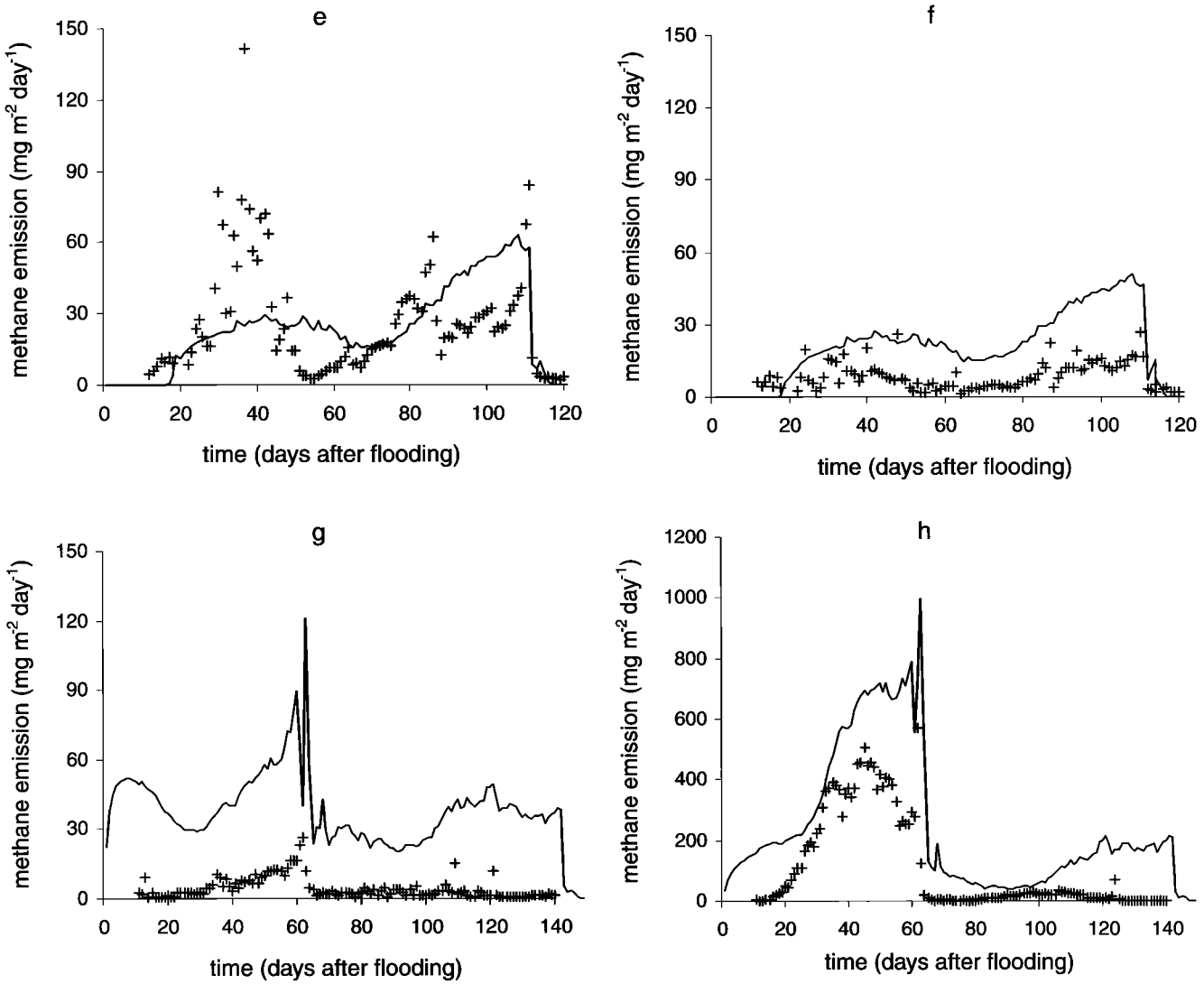


Figure 6. (continued)

automatically be taken into account as experimental data are used to estimate this time coefficient. The opposite will not occur because transport through the plant is faster than transport through the soil.

In the rhizosphere compartment, transport will mainly take place via plant-mediated transport. The time coefficient for plant-mediated transport was found to be smaller than 3 hours after the introduction of a temperature change [*Sass et al.*, 1991a] and 2–3 hours after an introduction of a change in light conditions [*Byrnes et al.*, 1995], respectively. The $\tau_{rhizosphere}$ is thus set at 2.5 hours in the model (Table 1).

There are no data available from which the time coefficient of transport by ebullition or diffusion through the bulk soil can be calculated directly. However, *Watanabe and Kimura* [1995] and *Kimura and Minami* [1995] calculated, using the same data set, that the maximum period between methane production and emission was 11–14 days at the start of the growing season. At the start of the season, transport through the soil dominates the methane transport completely [*Schütz et al.*, 1989b; *Wassmann et al.*, 1996]. In the model, it is therefore assumed that τ_{bulk} is 12.5 days (Table 1). From the large difference in time coefficients of the two compartments and the seasonal change in contribution of the compartments (equation (2)), the seasonal trends in conductance [*Hosono and Nouchi*, 1997] and in turnover times [*Watanabe and Kimura*, 1995; *Kimura and Minami*, 1995] can be calculated and understood.

In an aerobic period, at drainage, τ_{bulk} decreases as more pores for transport become available, releasing entrapped methane to the atmosphere. This results in a fast release of methane at the start of drainage that tails off afterward. This change in τ_{bulk} during the release can be described by an empirical beta function:

$$\tau_{bulk} = \frac{\text{release\_time}\frac{(v-1)!(v-1)!}{(v+w-1)!}}{\Delta r\_\text{time}^{v-1}(1-\Delta r\_\text{time})^{w-1}} \quad (14)$$

in which release_time is the period of methane release (7 days). Here v (5) and w (8) determine the curve shape and are estimated from *Denier van der Gon et al.* [1996]. The r_time is time/release_time, between 0 and 1.

2.5. Methane Oxidation

At aerobic/anaerobic interfaces, part of the methane is oxidized to CO_2 by methanotrophic bacteria in the presence of oxygen. Anaerobic methane oxidation is neglected for reasons

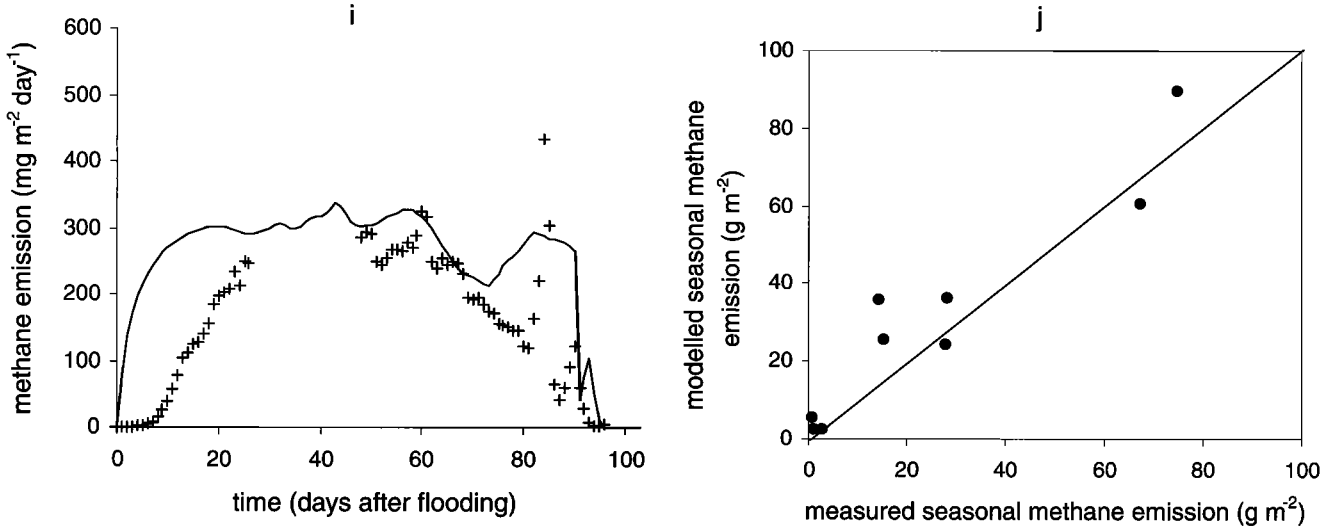


Figure 6. (continued)

given by *van Bodegom et al.* [2000]. Methane oxidation can be measured by a mass balance approach, comparing potential methane production in the absence of oxygen with the actual plant-mediated methane emission [e.g., *Holzapfel-Pschorn et al.*, 1985; *Sass et al.*, 1992]. This method overestimates methane oxidation as methanogenic activity is enhanced in such anaerobic incubations. Estimates with this method are much higher than those obtained by in situ experiments with 100% N_2, while these experiments produce an upper boundary for methane oxidation estimates [*Denier van der Gon and Neue*, 1996]. The second commonly used method is to measure methane oxidation in presence of specific inhibitors of methanotrophic activity. The problems with this method are that various inhibitors also partly inhibit methane production [*Frenzel and Bosse*, 1996; *Oremland and Culbertson*, 1992; *Oremland and Taylor*, 1975] and that the higher oxygen concentrations in the soil can also reduce methane production in various ways. These interfering effects seem to be limited in short-term incubations [*King*, 1996], and estimates obtained by this method are not higher than those obtained by in situ experiments with 100% N_2. Therefore specific inhibitor experiments are used to estimate methane oxidation.

Methane oxidation is limited by oxygen availability. Oxygen is released into the rhizosphere through ROL, which changes during the season [*Kludze et al.*, 1994; *Satpathy et al.*, 1997; *Wang et al.*, 1997] as a function of root activity. Seasonal changes in root exudation rates also depend on root activity. Therefore a similar Gaussian curve as for root exudation (equation (8)) is chosen for methane oxidation in the rhizosphere, adjusting parameter B and A (Table 1) such that the seasonal average oxidation in the rhizosphere equals to the average found by use of specific inhibitors, which is 32 ± 8% of the produced methane [*Banker et al.*, 1995; *Bosse and Frenzel*, 1997, 1998; *Denier van der Gon and Neue*, 1996; *Epp and Chanton*, 1995; *Gilbert and Frenzel*, 1995; *Sigren et al.*, 1997; *Tyler et al.*, 1997]. As this curve depends on root activity, which may be cultivar dependent, it may only be appropriate for IR72.

Oxygen diffuses into the bulk soil at the soil-water interface. At this interface, where methane and oxygen gradients meet, methane oxidation rates are high and fairly constant at 70–95% of the locally produced methane [*Banker et al.*, 1995; *Butterbach-Bahl et al.*, 1997; *Conrad and Rothfuss*, 1991; *Epp and Chanton*, 1995; *Gilbert and Frenzel*, 1995; *Schütz et al.*, 1989b]. However, only 10–20% of the methane emission from the bulk soil passes this soil-water interface by diffusion [*Rothfuss and Conrad*, 1993; *Schütz et al.*, 1989b]. The remaining emission from the bulk soil is transported by ebullition. Gas bubbles for ebullition are formed in anaerobic soil and hardly comes into contact with oxygen during transport to the atmosphere and will thus not be oxidized. Therefore only diffusive flux through the soil can lead to methane oxidation. The average fraction that is oxidized in the bulk soil can be calculated from these arguments at 37 ± 19% of the produced methane, on the basis of the data above. This fraction is not significantly different from the oxidation of 28 ± 11% of produced methane transported by ebullition and sediment diffusion, calculated by *Tyler et al.* [1997].

Table 2. Site Specific Input Parameters

	Maligaya	Los Baños	Beijing	Jakenan
Soil carbon content, %	1.21	1.86	0.99	0.48
Dithionite extractable iron, %	1.15	2.27	0.56	0.18
Daily temperature, °C	23.5–31.8	22.8–28.3	8.2–29.1	25.3–30.3
Rice cultivar	IR72	IR72	IR72	IR72
Yield, tons ha^{-1}	5.1–5.3	3.5–5.4	6.9	7.4
Water management	continuously flooded	continuously flooded	midseason drainage	continuously flooded
Growing season length, days	120–121	121	149	103
Fertilizer management	urea, KCl, solophos	urea	urea	urea

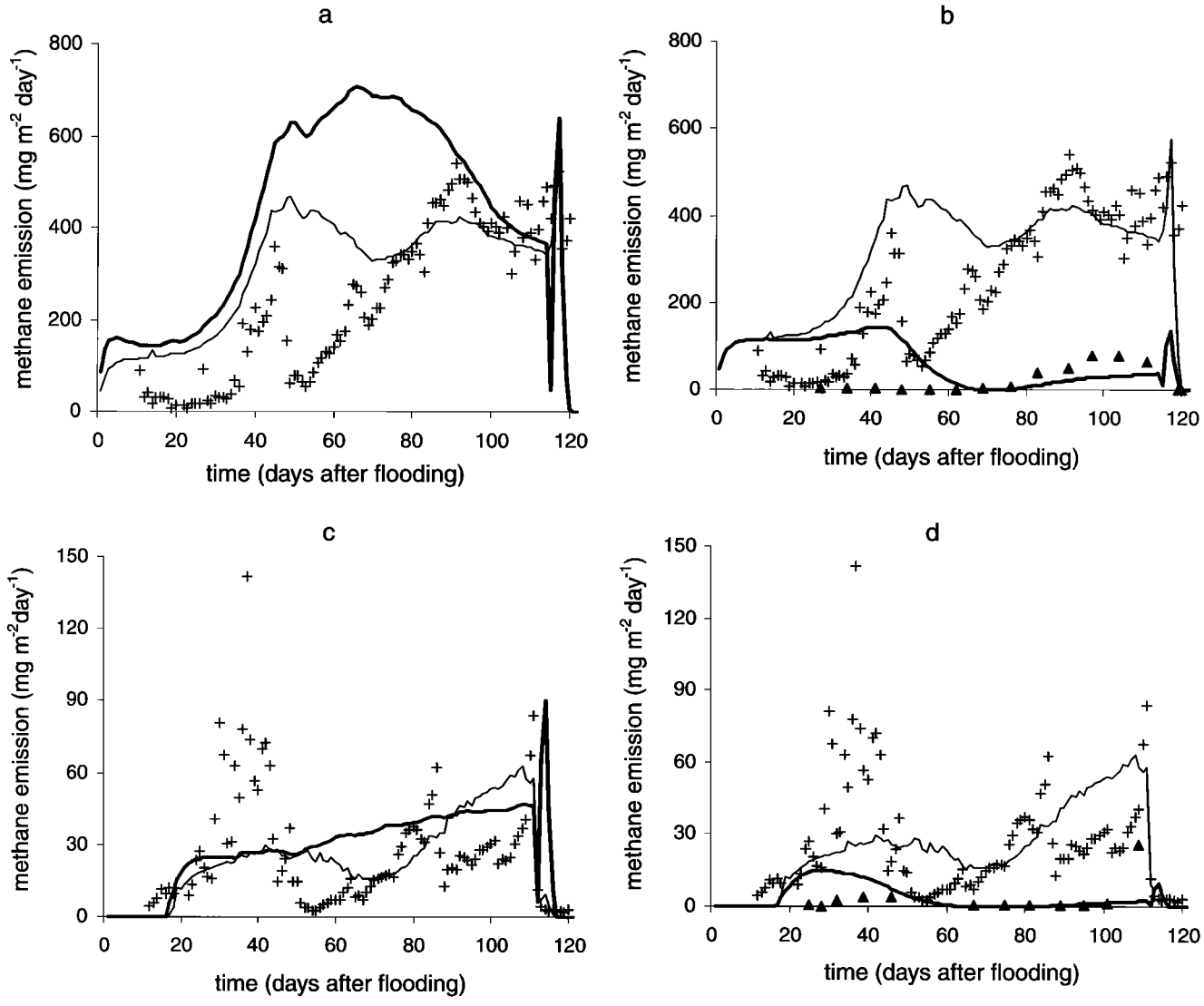


Figure 7. Sensitivity analysis of the model with (thin lines) and without (thick lines) the distinction of an explicit rhizosphere for (a) MA 96 control, (c) LB 97 control, and (e) LB 97 with straw. The modeled ebullition (thick lines) and modeled total methane emission (thin lines) are compared to data for total emission (pluses) and ebullition (triangles) for (b) MA 96 control, (d) LB 97 control, and (f) LB 97 with straw.

The remaining methane from each compartment is directly released from the interface into the atmosphere, thus assuming no transport limitation inside the plant or in the water layer on top of the soil. Methane emission is calculated as the sum of the methane released from the rhizosphere and the bulk soil. The model was written in Fortran Simulation Translator (FST) [*Rappoldt and van Kraalingen*, 1996] and is available upon request.

3. Model Validation

For model validation, model performance was compared to field data on daily methane emissions collected at various sites: Maligaya (MA) of the Philippine Rice Research Institute, Los Baños (LB) of the International Rice Research Institute in the Philippines, Beijing (BG) of the Institute of Crop Breeding and Cultivation in China, and Jakenan (JK) of the Central Research Institute for Food Crops in Indonesia (Figure 6). Diurnal patterns in methane emissions cannot be predicted by the model, given its objectives and simplified nature. At all sites, methane emissions were measured with an automatic closed chamber technique described in detail by *Wassmann et al.* [1994]. Site-specific experimental conditions are described elsewhere [*Metra-Corton et al.*, 1995, 2000; *Buendia et al.*, 2000; *Setyanto et al.*, 2000; *Wang et al.*, 2000].

All process parameters were kept at the constant values presented in Table 1 for all model runs. These values were not derived from the experimental data used for validation. These experimental sites represent therefore a truly independent validation of the model. All site-specific input parameters are shown in Table 2. Soil organic carbon and dithionite extractable iron can be found in soil maps. Daily temperature was measured at the site but can in general be found in weather inventories. The rice cultivar was in all cases IR72 because this is the only variety for which root activity data are known. Fertilization, water management, and

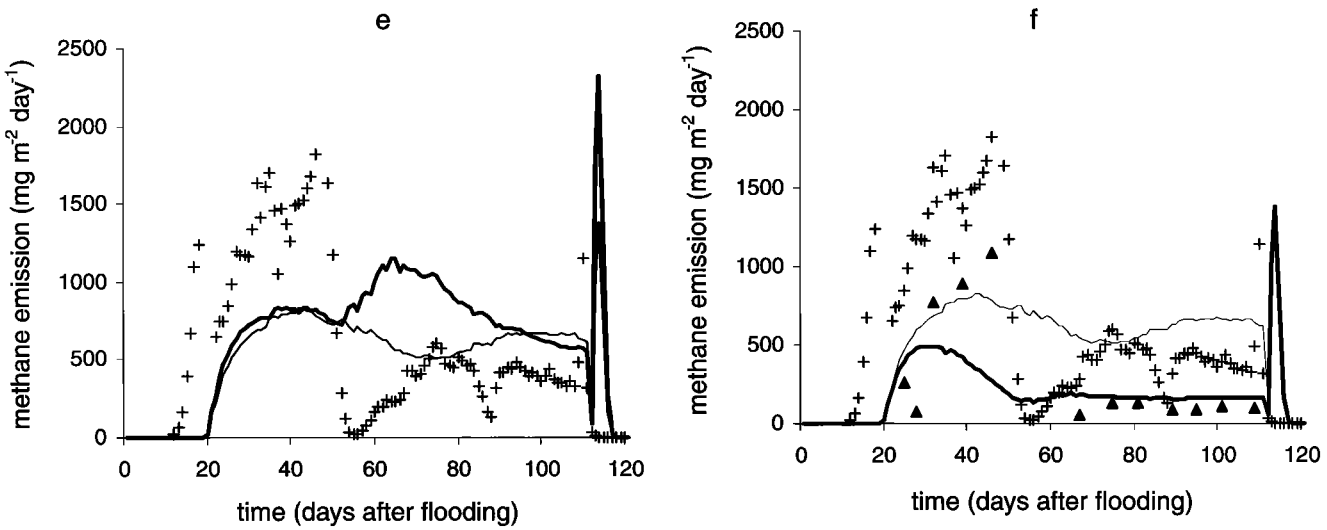


Figure 7. (continued)

length of the growing season were obtained from the site but can in general be found in agricultural databases. All sites were drained at the end of the season. All site-specific parameters can thus be obtained from generally available databases, facilitating extrapolation of this process-based model for use in regional and global studies. All other parameters were always kept at their default values presented in Table 1.

The model was validated under various conditions. Two seasons for Maligaya, wet season 1994 (MA94) data and wet season 1996 (MA96) data, were used in the validation set to test the representation of interseasonal variations in methane emissions by the model (Figure 6a and 6b). The model predicted well the different methane emissions in both seasons, which occurred mainly under influence of different temperatures. The effects of organic fertilization, in this case rice straw, was tested at various sites, at Maligaya (compare Figure 6b and 6c), Los Baños (compare Figure 6d and 6e), and at Beijing (compare Figure 6g and 6h). The addition of straw, and thus of extra carbon substrate, causes a tremendous increase in methane emissions especially during the 1st half of the season. The model could predict well both the magnitude and the timing of methane emission increase. The total increase is slightly underestimated at Los Baños and slightly overestimated at Beijing, but the differences with measured methane emissions are not significant (at $P < 0.05$). The performance of the model with a different inorganic fertilizer than urea, $CO(NH_2)_2$, was tested by including a treatment with $(NH_4)_2SO_4$. Sulfate additions reduce methane production as described by (10a–c) and lead to a reduction in both measured and modeled methane emissions (compare Figure 6e and 6f). The inhibiting effects of sulfate were slightly underestimated by the model, which is probably due to the neglect of the recycling of sulfurous compounds within the rice paddy.

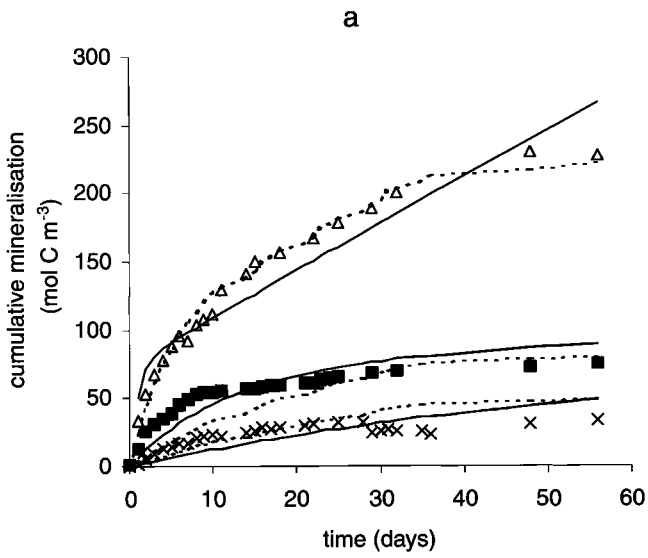
In the validation set, four sites in different countries differing tremendously in soil characteristics but with the same management and rice cultivar were compared (Figure 6b, 6e, 6g, and 6i). Both the absolute amounts and the patterns in the highly different methane emissions at the various sites could be well predicted by the model. Only the methane emissions predicted for BG97 were significantly higher (at $P < 0.05$) than the measured methane emissions, but BG97 control was a very low emitter and this overestimation will thus hardly influence model estimates if the model is extrapolated to regional scales.

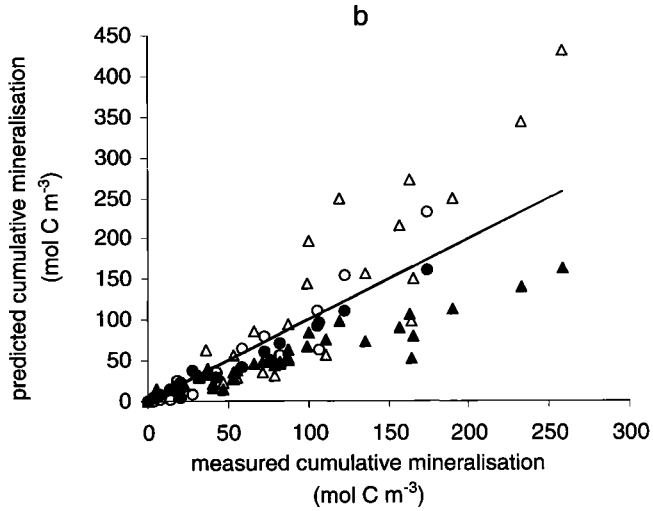
In all situations, except for BG97 control, the seasonal patterns in methane emission during the rice growth season were well described by the model and not significantly different from measured values (at $P < 0.05$). The various underestimations and overestimations by the model had no significant pattern across sites or treatments (at $P < 0.05$) and are probably caused by heterogeneities or site-specific characteristics not captured by the model, given the fact that all process parameters were kept constant during all validations. Modeled seasonal methane emissions did not differ significantly (at $P < 0.05$) from measured seasonal methane emissions (Figure 6j) and had a coefficient of variation of only 8% with the measured emission and a Pearson correlation coefficient of 0.95, while emissions varied up to 2 orders of magnitude.

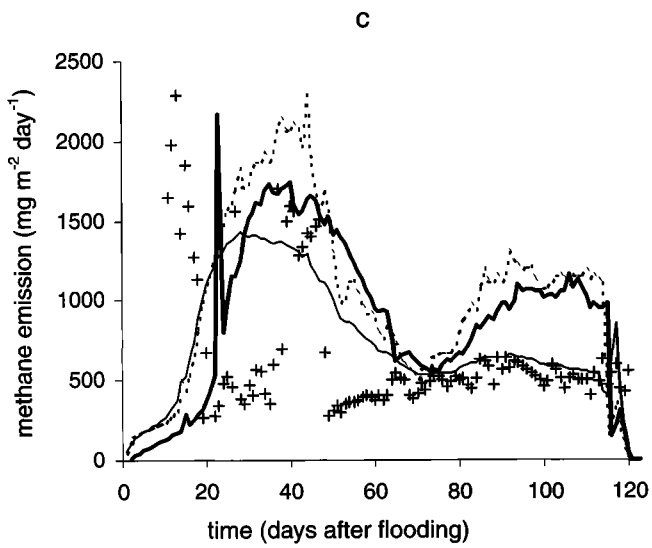
4. Sensitivity Analysis on Model Assumptions

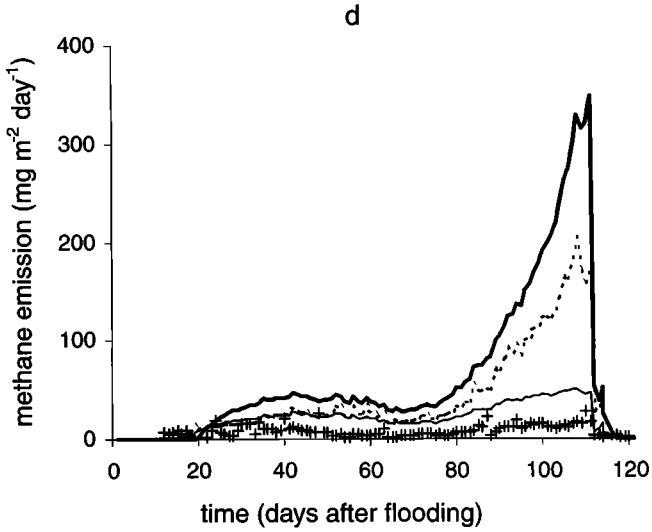
During the development of a process-based model some assumptions have been made on process descriptions. In this section we evaluate the influence of different model assumptions mentioned in section 2. The most important assumption of the described model is that the importance of rice plants on methane emissions is large enough to justify a distinction between a

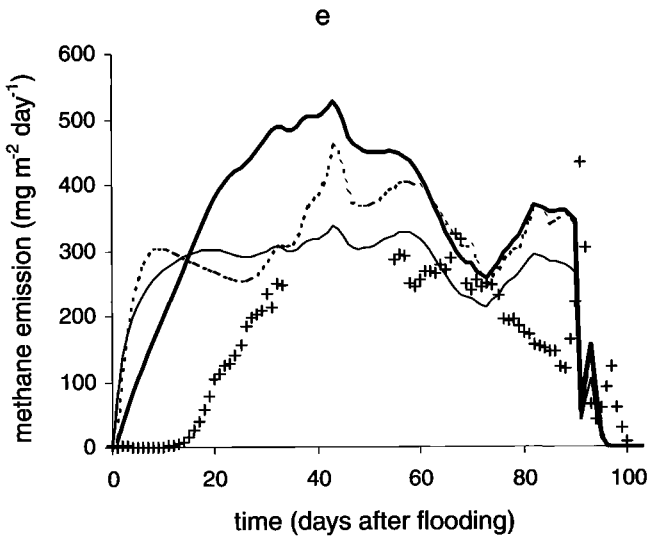
Figure 8. Sensitivity analysis of the model on soil organic matter mineralization formulations. (a) Calibration of *Parton et al.* [1987] mineralization model (dashes) and two-compartment mineralization model (lines) with measured cumulative mineralization in an incubation study with rice paddy soil at 14°C (crosses), 20°C (filled squares), and 30°C (open triangles). (b) Validation of the mineralization models based on *Parton et al.* [1987] (closed symbols) and the two-compartment model (open symbols) with independent data presented by *Tsutsuki and Ponnamperuma* [1987] (triangles) and *Inubushi et al.* [1997] (circles). Influence of use of the mineralization model based on *Parton et al.* [1987] (thick lines) and the two-compartment mineralization model (dashes) compared to the default model (thin lines) and measured data (pluses) for (c) MA 96 with straw, (d) LB 97 with $(NH_4)_2SO_4$, and (e) JK 96 control.


a
cumulative mineralisation (mol C m-3)
time (days)


b
predicted cumulative mineralisation (mol C m-3)
measured cumulative mineralisation (mol C m-3)


c
methane emission (mg m-2 day-1)
time (days after flooding)


d
methane emission (mg m-2 day-1)
time (days after flooding)


e
methane emission (mg m-2 day-1)
time (days after flooding)

rhizosphere and a bulk soil compartment. This assumption was tested by reformulating the model with one compartment with a uniform distribution of carbon substrates, while keeping the total carbon release equal to the default model. Transport was spatially averaged by applying an average τ to (13). An average methane oxidation fraction was derived from the oxidation fraction of both compartments. The results are presented in Figure 7a, 7c, and 7e. Seasonal methane emissions increase 20–52% if one compartment is used, while total carbon substrate release was taken the same in both models. Methane emissions increase especially in the middle of the season, when methane oxidation in the rhizosphere is the largest. This influence by ROL dynamics is taken away in the one-compartment model, leading to poorer methane emission predictions.

Indirect support for the distinction between a rhizosphere and a bulk soil was obtained by showing the contribution of the bulk soil and of the rhizosphere to the overall methane emission. The independent estimate of ebullition, taken as the emission from the bulk soil, can be used to validate the concepts of the model by comparison with measured ebullition data. Results of the model are shown in Figure 7b, 7d, and 7f for the same experiments as presented in Figure 7a, 7c, and 7e. Both modeled and measured ebullition have their highest contribution at the start and end of the season, when plant influence is small. Modeled ebullition contributed 15–22% to the total methane emission at treatments with inorganic fertilizer additions, with two examples in Figure 7b and 7d, which is a reasonable value if no extra organic fertilizers are added [*Byrnes et al.*, 1995; *Nouchi et al.*, 1994; *Schütz et al.*, 1989b]. With the addition of extra rice straw, ebullition contributed 32–53% to the total methane emission and was 39% in MA96 (Figure 7f). These estimates are also comparable to sites to which organic fertilizer was added [*Denier van der Gon and Neue*, 1995a; *Wassmann et al.*, 1996]. Moreover, the overall conductance, which can be calculated from the compartment contributions and their respective transport time coefficients, shows the same trends and has the same order of magnitude as the conductance presented by *Hosono and Nouchi* [1997]. Unfortunately, an exact comparison is not possible, as *Hosono and Nouchi* [1997] did not present the number of shoots at each sampling. These results show that the model can predict methane transport characteristics and that the division into two compartments yields a reasonable methane transport description.

One of the most sensitive factors influencing methane emissions from rice paddies is the production of carbon substrates [*van Bodegom et al.*, 2000]. If no extra straw is added, the contribution of soil organic matter mineralization to total carbon substrate release varies from 45% at the low soil carbon site Jakenan to 68% at the high-carbon site Los Baños. The remainder is either directly, via root exudation and root decomposition, or indirectly, via rice straw, derived from plants. Given the importance of soil mineralization, it is unfortunate that no mineralization model has been developed specifically for anaerobic conditions. In this study, the general model described by *Yang* [1996] was used as default as the description is independent of aerobic or anaerobic conditions and because it uses the least number of parameters. Two other mineralization models were used to test the effect of soil mineralization description on methane emission predictions, (1) a two-pools model and (2) the CENTURY model [*Parton et al.*, 1987], which was applied by *Cao et al.* [1995].

The two-pools model assumes that soil organic carbon consists of two pools, each with a constant relative decomposition rate. The two pools do not interact, and the sum of the pools is equal to the total soil organic carbon content. With this two-pools model, (3) and (4) simplify to

$$P_{\min} = C_{\min}(F_{\text{fast}}K_{\text{fast}}e^{-K_{\text{fast}}\text{time}} + (1 - F_{\text{fast}})K_{\text{slow}}e^{-K_{\text{slow}}\text{time}}) \quad (15)$$

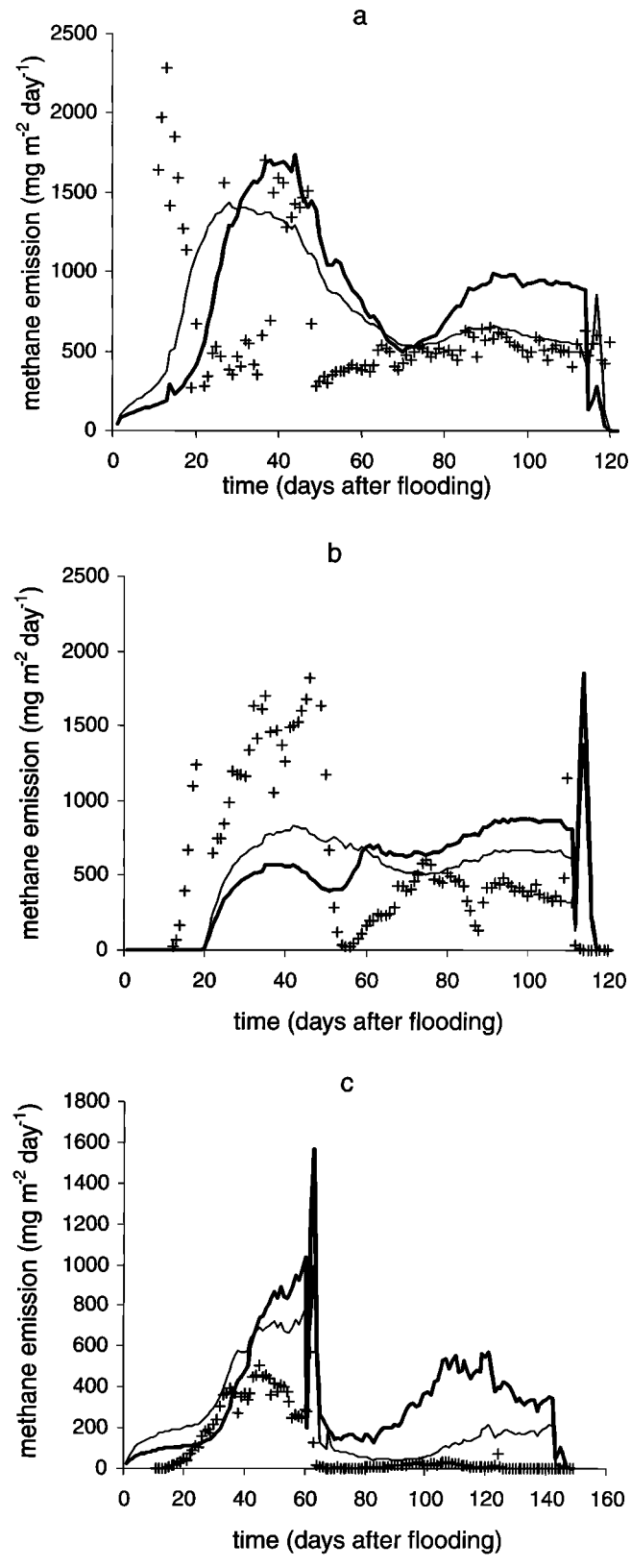
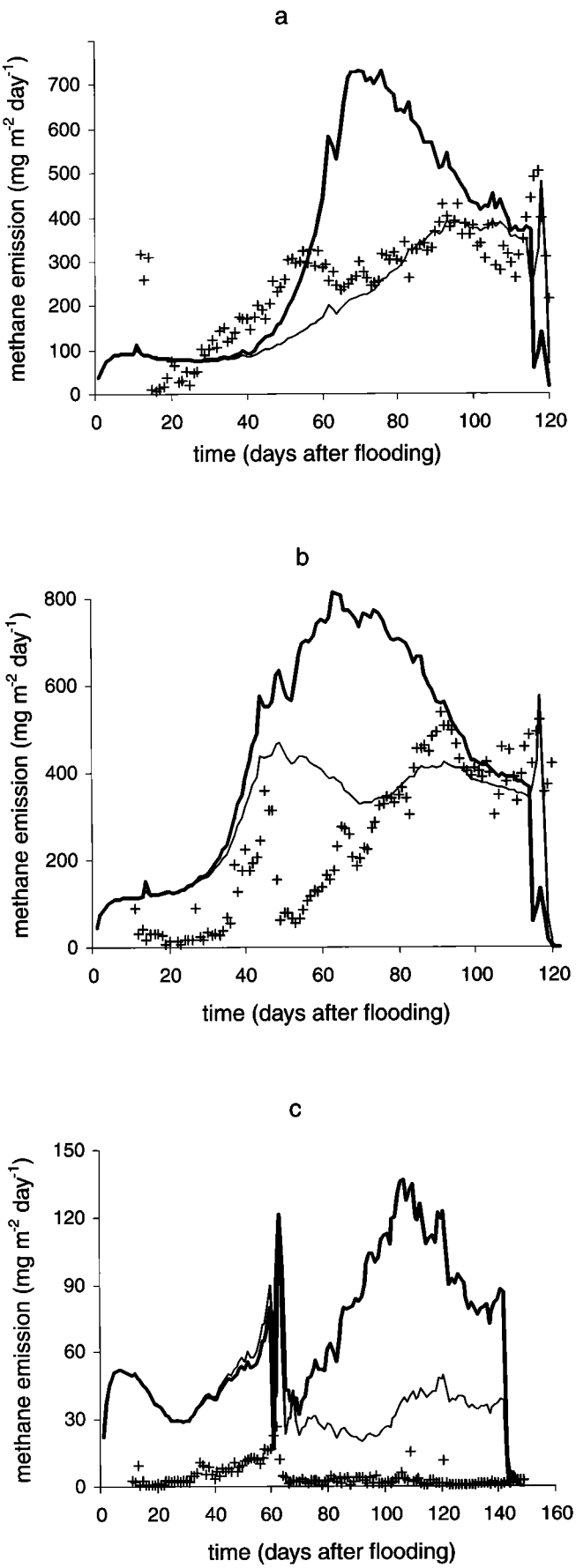


Figure 9. Sensitivity of the model on the description of rice straw decomposition. A description with a constant relative decomposition rate for rice straw (thick lines) is compared to the default model (thin lines) and measured data (pluses) for (a) MA 96 with straw, (b) LB 97 with straw, and (c) BG 97 with straw.



in which F_{fast} (−) is the fraction of the organic matter pool that is assigned to the fast pool and K_{fast} and K_{slow} are decomposition constants (s^{-1}) of the fast pool and the slow pool, respectively. These three parameters were all fitted (Figure 8a) to experimental data from soil incubation studies [*van Bodegom and Stams*, 1999]: $F_{fast} = 0.022$ (−), $K_{fast} = 1.21 \times 10^{-5}$ (s^{-1}), and $K_{slow} = 1.25 \times 10^{-8}$ (s^{-1}).

The CENTURY model was developed for aerobic soils. Parameter values of this model can thus not be used directly for anaerobic conditions. To avoid too many fitted parameters, pool distribution ratios were used from the CENTURY model. The distribution of plant residue between metabolic and structural carbon pools was estimated from the ratio lignin/nitrogen [*Parton et al.*, 1987, Equation (2)] using data for rice plant characteristics presented by *Saini* [1989]. While maintaining the same ratio in litter decomposition constants, the plant decomposition constants were estimated from data on rice straw decomposition, mentioned above. Conversion ratios of decomposing organic matter to CO_2 and decomposition constants for the soil carbon pools corrected for texture, which is known to influence methane emissions but which is not part of the *Yang* [1996] model, were obtained from *Parton et al.* [1987]. Only one decomposition constant ($K_{d,\text{passive pool}}$) remained to be fitted. Fluctuating moisture effects are absent in a continuously flooded rice paddy soil. Temperature effects were described by a calibrated Q_{10} value to allow comparison with the default model. Finally, the three initial soil carbon pool sizes had to be calibrated, with the constraint that their sum is equal to the total organic carbon amount. This leaves two pool fractions to be calibrated: $F_{\text{passive pool}}$ and $F_{\text{slow pool}}$. All four parameters were optimized simultaneously against experimental soil incubation data [*van Bodegom and Stams*, 1999] for the smallest mean square error and the smallest change in pool size fractions during the season (Figure 8a). This led to $K_{d,\text{ passive pool}} = 0.7\ 10^{-9}$ (s^{-1}), $Q_{10} = 2.71$, $F_{\text{passive pool}} = 0.738$ (−), and $F_{\text{slow pool}} = 0.122$ (−).

Both models could reasonably describe anaerobic soil mineralization rates in rice paddy soils presented by *Tsutsuki and Ponnamperuma* [1987] and *Inubushi et al.* [1997], although the two-pools model overestimated mineralization rates at high fertilization (Figure 8b). With the two-pools model, methane emissions were 14–102% higher than for the default model (examples given in Figure 8c, 8d, and 8e). The overestimation mainly occurs in the 2nd half of the season when predicted mineralization rates began to deviate from measured mineralization rates (Figure 8a). The modified CENTURY model is also less applicable than the default model, even though it was calibrated for anaerobic conditions. The deviations are hard to explain and may be coincidental or due to the fact that CENTURY was developed for long-term predictions in aerobic systems. In absence of organic fertilizers the CENTURY model led to 13–270% higher methane emissions than for the default model (examples given in Figure 8d and 8e). With organic fertilizers, the CENTURY model performed similarly well as the default model (example given in Figure 8c) but still produced 18–28% higher emission estimates. Anaerobic mineralization modeling deserves more attention.

Rice straw becomes an important source of carbon substrate if it is added as organic fertilizer, 50–62% of the total carbon release according to the model. In the model, it was assumed that

Figure 10. Sensitivity of the model on the description of methane oxidation. A description with a constant percentage of produced methane that is oxidized (thick lines) is compared to the default model (thin lines) and measured data (pluses) for (a) MA 94 control, (b) MA 96 control, and (c) BG 97 control.

organic fertilizers decompose according to (7). Normally, however, a constant relative decomposition rate, (6), for organic fertilizers is assumed. As a sensitivity analysis, the model was run with a constant relative decomposition rate for organic fertilizers based on literature data, mentioned above, with incubation periods $\leq$ 120 days. This change in the model hardly affected the outcome if no organic fertilizers are added (results not shown). With the addition of organic fertilizers (Figure 9), the effects were larger and led to 9–17% higher emissions. Especially during the 2nd half of the season, methane emissions were overestimated by the model with a constant relative decomposition rate. This can be explained by the fact that at that point in the season easily accessible carbon has been depleted, leading to decreased decomposition rates and thus to overestimations when a constant relative decomposition rate is used.

In various models [*James*, 1993; *Grant*, 1998; *Segers and Kengen*, 1998], competition between methane-producing bacteria and other anaerobic bacteria is described by Michaelis-Menten kinetics. In this model, the competition was simplified to (10a–c). Inclusion of Michaelis-Menten kinetics would only affect the competition with sulfate reducers, as nitrate and ferric iron reducers outcompete methanogens under all conditions. Sulfate reduction is only of minor importance for the seasonal electron balance [*van Bodegom and Stams*, 1999; *Inubushi et al.*, 1984], and methane emissions are hardly affected even in an extreme scenario of outcompetition of methanogens by sulfate reducers [*van Bodegom et al.*, 2000]. The simplification of (10a–c) is thus reasonable.

A more important assumption, as was already indicated in section 3, is that there is no reoxidation of electron acceptors in a flooded rhizosphere. This implicitly means that only methanotrophs and heterotrophic respiration consume the oxygen available in the rhizosphere. Unfortunately, our model cannot test this important assumption as the model does not distinguish gradients and because it is not possible to determine oxygen limited conversion rates with this model. The model of *Segers and Leffelaar* [2001], however, takes into account diffusion and oxygen limitations. According to that model, reoxidation of electron acceptors is not important under oxygen limited circumstances. The assumption seems thus reasonable, although quantitative verification is not possible with the present model.

The final assumption in the model is that methane oxidation is linearly related to root activity, (8). This assumption was necessary due to a lack of quantitative data on changes in methane oxidation or ROL during the season. Only an average methane oxidation percentage could be calculated from the data. If the model is run with this average instead of an activity curve, the trends in methane emission are strongly influenced (Figure 10) and lead to major overestimations of methane emissions in the middle of the season, when root activity is highest. Seasonal methane emissions were 8–57% higher than for the default model. It is thus necessary to take into account the seasonal changes in methane oxidation, as is done in the default model. Root exudation and ROL are not only temporally dynamic but moreover depend on the rice cultivar. Unfortunately, there are no quantitative cultivar specific data, which limits the validation possibilities of the model for non-IR cultivars. More data are needed on these root activity characteristics.

5. Concluding Remarks

In this paper, a model for methane emission predictions from rice paddies at the field scale level is described. Because of a lack of mechanistic knowledge, not all processes could be described fully mechanistically. Therefore the descriptions of most important system properties were kept simple to achieve a well-balanced model, even though in some cases more mechanistic knowledge is available. The model was validated, without fitting, with data from independent field experiments at various sites in Asia. With only a few site-specific input parameters (Table 2), the seasonal dynamics in methane emissions could be well described. Total seasonal methane emission was not significantly different from measured seasonal emissions (at $P < 0.05$), while the different conditions had led to seasonal emissions differing over 2 orders of magnitude.

The sensitivity analysis also showed that the model assumptions were reasonable. The most important assumption was the model simplification to distinguish two compartments, a rhizosphere and a bulk soil compartment. The model performed worse without such a division, showing the importance of heterogeneities introduced by the plant, while, of the models referred to, only *Arah and Stephen* [1998] and *Walter et al.* [1996] describe this heterogeneity, using a more physical approach. None of the models, however, include other heterogeneities. This omission probably had a major influence, in combination with site-specific variabilities, on the deviations between model and experiment. The sensitivity analysis also showed the importance of a proper quantitative description on anaerobic organic matter decomposition processes. Modeling these processes thus deserves more attention to improve future models also because the empirical models mentioned in the introduction do not account for this soil process. Another important aspect of the model is the competition for substrate by alternative electron acceptors, which is, of the models referred to, only included in the model of *James* [1993]. Neglect of this competition severely overestimates methane emissions at the start of the season especially in soils high in alternative electron acceptors, like Los Baños, for which this competition is important. A description of Eh independent of soil type will thus not suffice. In the model, it was assumed and argued that reoxidation of electron acceptors is not important, but it deserves more attention especially for soils high in alternative electron acceptors and for rain-fed systems. The sensitivity analysis also showed that it is important to account for seasonal changes in methane oxidation, indicating that there is a need to understand this process. In the models of *Huang et al.* [1998] and *Cao et al.* [1995], a different oxidation dynamics was used, leading to an underestimation of methane emissions at the end of the season (results not shown).

From the model validation and sensitivity analysis we conclude that the assumptions made in this model are reasonable because methane emissions are well predicted. The model can be used for larger-scale applications for flooded rice paddies because it makes use of general process relations and because it needs few site- specific parameters. The site-specific parameters can be obtained from general databases, facilitating application of the model. Caution is needed when the model is applied to rice cultivars for which the model was not parameterized.

Acknowledgments. The authors thank Jan Goudriaan, Fons Stams, and Peter Leffelaar for useful comments. The research was supported financially by the Dutch National Research Program on Global Air Pollution and Climate Change.

References

Acharya, C. N., Studies on the anaerobic decomposition of plant materials, III, Comparison of the course of decomposition of rice straw under anaerobic, aerobic and partially aerobic conditions, *Biochem. J.*, *29*, 1116–1120, 1935.

Achtnich, C., A. Schuhmann, T. Wind, and R. Conrad, Role of interspecies H_2 transfer to sulfate and ferric iron-reducing bacteria in anoxic paddy soil, *FEMS Microbiol. Ecol.*, *16*, 61–70, 1995a.

Achtnich, C., F. Bak, and R. Conrad, Competition for electron donors among nitrate reducers, ferric iron reducers, sulfate reducers and methanogens in anoxic paddy soil, *Biol. Fertil. Soils*, *19*, 65–72, 1995b.

Arah, J. R. M., and K. D. Stephen, A model of the processes leading to methane emission from peatland, *Atmos. Env.*, *32*, 3257–3264, 1998.

Armstrong, W., and P. M. Beckett, Internal aeration and the development of stelar anoxia in submerged roots: A multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere, *New. Phytol.*, *105*, 221–245, 1987.

Banker, B. C., H. K. Kludze, D. P. Alford, R. D. Delaune, and C. W. Lindau, Methane sources and sinks in paddy rice soils: Relationship to emissions, *Agric., Ecosys. Env.*, *53*, 247–251, 1995.

Beyrouty, C. A., B. R. Wells, R. J. Norman, J. N. Marvel, and J. A. Pillow, Root growth dynamics of a rice cultivar grown at two locations, *Agron. J.*, *80*, 1001–1004, 1988.

Bosse, U., and P. Frenzel, Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*), *Appl. Env. Microbiol.*, *63*, 1199–1207, 1997.

Bosse, U., and P. Frenzel, Methane emissions from rice microcosms: The balance of production, accumulation and oxidation, *Biogeochemistry*, *41*, 199–214, 1998.

Buendia, L. V., R. Wassmann, R. S. Lantin, H. U. Neue, A. M. Javellana, C. S. Bueno, N. Nocon, A. Umali, and L. A. Lubigan, A five-year study of methane emissions from rice fields in Los Baños (Philippines), *Nutrient Cycling Agroecosys.*, in press, 2000.

Butterbach-Bahl, K., Mechanismen der Produktion und Emission von Methan in Reisfeldern: Abhängigkeit von Feldüngung und angebauter Varietät, Diss. Tech. Univ. München. Schriftenreihe des Fraunhofer Inst. für Atmos. Umweltforschung, Wiss Verl. Mauraun, Frankfurt, 1992.

Butterbach-Bahl, K., H. Papen, and H. Rennenberg, Impact of gas transport through rice cultivars on methane emission from rice paddy fields, *Plant Cell Environ.*, *20*, 1175–1183, 1997.

Byrnes, B. H., E. R. Austin, and B. K. Tays, Methane emissions from flooded rice soils and plants under controlled conditions, *Soil Biol. Biochem.*, *27*, 331–339, 1995.

Cao, M., J. B. Dent, and O. W. Heal, Modeling methane emissions from rice paddies, *Global Biogeochem. Cycles*, *9*, 183–195, 1995.

Conrad, R., and F. Rothfuss, Methane oxidation in the soil surface layer of a flooded rice field and the effect of ammonium, *Biol. Fertil. Soils*, *12*, 28–32, 1991.

Conrad, R., F. Bak, H. J. Seitz, B. Thebrath, H. P. Mayer, and H. Schütz, Hydrogen turnover by psychrotrophic homoacetogenic and mesophilic bacteria in anoxic paddy soil and lake sediment, *FEMS Microbiol. Ecol.*, *62*, 285–294, 1989a.

Conrad, R., H. P. Mayer, and M. Wüst, Temporal change of gas metabolism by hydrogen-syntrophic methanogenic bacterial associations in anoxic paddy soil, *FEMS Microbiol. Ecol.*, *62*, 265–274, 1989b.

Denier van der Gon, H. A. C., and H. U. Neue, Influence of organic matter incorporation on the methane emission from a wetland rice field, *Global Biogeochem. Cycles*, *9*, 11–22, 1995a.

Denier van der Gon, H. A. C., and H. U. Neue, Methane emission from a wetland rice field as affected by salinity, *Plant Soil*, *170*, 307–313, 1995b.

Denier van der Gon, H. A. C., and H. U. Neue, Oxidation of methane in the rhizosphere of rice plants, *Biol. Fertil. Soils*, *22*, 359–366, 1996.

Denier van der Gon, H. A. C., N. van Breemen, H. U. Neue, R. S. Lantin, J. B. Aduna, M. C. R. Alberto, and R. Wassmann, Release of entrapped methane from wetland rice fields upon soil drying, *Global Biogeochem. Cycles*, *10*, 1–7, 1996.

Devai, I., and R. D. Delaune, Light hydrocarbon production in freshwater marsh soil as influenced by soil redox conditions, *Water Air Soil Pollut.*, *88*, 39–46, 1996.

Drenth, H., H. F. M. ten Berge, and F. W. Meijboom, Effects of growth medium on porosity and branching of rice roots (*Oryza Sativa* L.), in *Simulation and Systems Analysis for Rice Production (SARP)*, edited by F. W. T. Penning de Vries et al., pp. 162–175, Pudoc, Wageningen, Netherlands, 1991.

Epp, M. A., and J. P. Chanton, Rhizospheric methane oxidation determined via the methyl fluoride inhibition technique, *J. Geophys. Res.*, *98*, 18,413–18,422, 1995.

Fetzer, S., and R. Conrad, Effects of redox potential on methanogenesis by *Methanosarcina barkeri*, *Arch. Microbiol.*, *160*, 108–113, 1993.

Frenzel, P., and U. Bosse, Methyl fluoride, an inhibitor of methane oxidation and methane production, *FEMS Microbiol. Ecol.*, *21*, 25–36, 1996.

Frenzel, P., B. Thebrath, and R. Conrad, Oxidation of methane in the oxic surface layer of a deep lake sediment (Lake Constance), *FEMS Microbiol. Ecol.*, *73*, 149–158, 1990.

Gilbert, B., and P. Frenzel, Methanotrophic bacteria in the rhizosphere of rice microcoms and their effect on porewater methane concentration and methane emissions, *Biol. Fertil. Soils*, *20*, 93–100, 1995.

Grant, R. F., Simulation of methanogenesis in the mathematical model ECOSYS, *Soil Biol. Biochem.*, *30*, 883–896, 1998.

Holzapfel-Pschorn, A., R. Conrad, and W. Seiler, Production, oxidation and emission of methane in rice paddies, *FEMS Microbiol. Ecol.*, *31*, 343–351, 1985.

Holzapfel-Pschorn, A., R. Conrad, and W. Seiler, Effects of vegetation on the emission of methane from submerged paddy soil, *Plant Soil*, *92*, 223–233, 1986.

Hosono, T., and I. Nouchi, The dependence of methane transport in rice plants on the root zone temperature, *Plant Soil*, *191*, 233–240, 1997.

Houghton, J. T., L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Marskell, *Climate Change 1995. The Science of Climate Change*, 1st ed, Cambridge Univ. Press, New York, 1996.

Huang, Y., R. L. Sass, and F. M. Fisher Jr., A semi-empirical model of methane emission from flooded rice paddy soils, *Global Change Biol.*, *4*, 247–268, 1998.

Inubushi, K., H. Wada, and Y. Takai, Easily decomposable organic matter in paddy soil, IV, Relationship between reduction process and organic matter decomposition, *Soil Sci. Plant Nutrient*, *30*, 189–198, 1984.

Inubushi, K., K. Hori, S. Matsumoto, and H. Wada, Anaerobic decomposition of organic carbon in paddy soil in relation to methane emission to the atmosphere, *Water Sci. Tech.*, *36*, 523–530, 1997.

James, R. T., Sensitivity analysis of a simulation model of methane flux from the Florida Everglades, *Ecol. Modell.*, *68*, 119–146, 1993.

Jenkinson, D. S., D. D. Harkness, E. D. Vance, D. E. Adams, and A. F. Harrison, Calculating net primary production and annual input of organic matter to soil from the amount and radiocarbon content of soil organic matter, *Soil Biol. Biochem.*, *24*, 295–308, 1992.

Kang, S.-Y., S. Morita, and K. Yamazaki, Root growth and distribution in some Japonica-Indica hybrid and Japonica type rice cultivars under field conditions, *Jpn. J. Crop Sci.*, *63*, 118–124, 1994.

Kimura, M., and K. Minami, Dynamics of methane in rice fields, in *Climate Change and Rice*, edited by S. Peng et al., pp. 33–45, Springer-Verlag, New York, 1995.

King, G. M., In situ analyses of methane oxidation associated with the roots and rhizomes of a bur reed, *Sparganium eurycarpum*, in a Maine wetland, *Appl. Env. Microbiol.*, *62*, 4548–4555, 1996.

Kirk, G. J. D., and J. L. Solivas, On the extent to which root properties and transport through the soil limit nitrogen uptake by lowland rice, *Eur. J. Soil Sci.*, *48*, 613–621, 1997.

Klüber, H. D., and R. Conrad, Effects of nitrate, nitrite, NO and N_2O on methanogenesis and other redox processes in anoxic rice field soil, *FEMS Microbiol. Ecol.*, *25*, 301–318, 1998.

Kludze, H. K., and R. D. Delaune, Gaseous exchange and wetland plant response to soil redox intensity and capacity, *Soil Sci. Soc. Am. J.*, *59*, 939–945, 1995.

Kludze, H. K., R. D. Delaune, and W. H. Patrick Jr., A colorimetric method for assaying dissolved oxygen loss from container-grown rice roots, *Agron. J.*, *86*, 483–487, 1994.

Krumböck, M., and R. Conrad, Metabolism of position-labelled glucose in anoxic methanogenic paddy soil and lake sediment, *FEMS Microbiol. Ecol.*, *85*, 247–256, 1991.

Lovley, D. R., and E. J. P. Phillips, Organic matter mineralization with reduction of ferric iron in anaerobic sediments, *Appl. Env. Microbiol.*, *51*, 683–689, 1986.

Lovley, D. R., and E. J. P. Phillips, Competitive mechanisms for inhibition of sulfate reduction and methane production in the zone of ferric iron reduction in sediments, *Appl. Env. Microbiol.*, *53*, 2636–2641, 1987.

Lu, Y., R. Wassmann, H. U. Neue, and C. Huang, Impact of phosphorus supply on root exudation, aerenchyma formation and methane emission of rice plants, *Biogeochemistry*, *47*, 203–218, 1999.

Masscheleyn, P. H., R. D. Delaune, and W. H. Patrick Jr., Methane and nitrous oxide emissions from laboratory measurements of rice soil suspension: Effect of soil oxidation-reduction status, *Chemosphere*, *26*, 251–260, 1993.

Mayer, H. P., and R. Conrad, Factors influencing the population of methanogenic bacteria and the initiation of methane production upon flooding of paddy soil, *FEMS Microbiol. Ecol.*, *7*, 103–112, 1990.

Metra-Corton, T. M., J. B. Bajita, C. A. Asis Jr., and R. R. Pamplona, Methane emission from an irrigated Philippine paddy field subjected to several fertilizer treatments, *Phillip. J. Crop Sci.*, *20*, 39–55, 1995.

Metra-Corton, T. M., J. B. Bajita, F. S. Grospe, R. R. Pamplona, C. A. Asis Jr., R. Wassmann, and R. S. Lantin, Methane emission from irrigated and intensively managed rice fields in Central Luzon (Philippines), *Nutrient Cycl. Agroecosys.*, in press, 2000.

Minami, K., Effects of agricultural management on methane emission from rice paddies, rep., Nat. Inst. of Agro-environmental Sci., Tsukuba, Japan, 1989.

Minoda, T., and M. Kimura, Contribution of photosynthesized carbon to the methane emitted from paddy fields, *Geophys. Res. Lett.*, *21*, 2007–2010, 1994.

Minoda, T., M. Kimura, and E. Wada, Photosynthates as dominant source of CH_4 and CO_2 in soil water and CH_4 emitted to the atmosphere from paddy fields, *J. Geophys. Res.*, *101*, 21,091–21,097, 1996.

Murthy, N. B. K., S. P. Kale, and K. Raghu, Mineralization of ^{14}C-labeled rice straw in aerobic and anaerobic clay soils as influenced by insecticide treatments, *Soil Biol. Biochem.*, *23*, 857–859, 1991.

Neue, H. U., and H. W. Scharpenseel, Decomposition pattern of ^{14}C-labeled rice straw in aerobic and submerged rice soils of the Philippines, *Sci. Total Env.*, *62*, 431–434, 1987.

Nouchi, I., T. Hosono, K. Aoki, and K. Minami, Seasonal variation in methane flux from rice paddies associated with methane concentration in soil water, rice biomass and temperature and its modelling, *Plant Soil*, *161*, 195–208, 1994.

Oremland, R. S., and C. W. Culbertson, Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor, *Nature*, *356*, 421–423, 1992.

Oremland, R. S., and B. F. Taylor, Inhibition of methanogenesis in marine sediments by acetylene and ethylene: Validity of the acetylene reduction assay for anaerobic microcosms, *Appl. Env. Microbiol.*, *30*, 707–709, 1975.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains grasslands, *Soil Sci. Soc. Am. J.*, *51*, 1173–1179, 1987.

Paustian, K., W. J. Parton, and J. Persson, Modelling soil organic matter in organic-amended and nitrogen fertilized long-term plots, *Soil Sci. Soc. Am. J.*, *56*, 476–488, 1992.

Peters, V., and R. Conrad, Methanogenic and other strictly anaerobic bacteria in desert soil and other oxic soils, *Appl. Env. Microbiol.*, *61*, 1673–1676, 1995.

Rappoldt, C., and D. W. G. van Kraalingen, The Fortran Simulation Translator. FST version 2.0. Introduction and reference manual, in *Quantitative Approaches in Systems Analysis*, Agric. Res. Inst. for Agrobiology and Soil Fert. (AB-DLO), Netherlands, 1996.

Ratering, S., and R. Conrad, Effects of short-term drainage and aeration on the production of methane in submerged rice soil, *Global Change Biol.*, *4*, 397–407, 1998.

Rothfuss, F., and R. Conrad, Vertical profiles of CH_4 concentrations, dissolved substrates and processes involved in CH_4 production in a flooded Italian rice field, *Biogeochemistry*, *18*, 137–152, 1993.

Saini, R. C., Mass loss and nitrogen concentration changes during the decomposition of rice residues under field conditions, *Pedobiologica*, *33*, 229–235, 1989.

Sass, R. L., and F. M. Fisher, Methane emissions from Texas rice fields: A five-year study, in *Climate Change and Rice*, edited by S. Peng et al., pp. 46–59, Springer-Verlag, New York, 1995.

Sass, R. L., F. M. Fisher, P. A. Harcombe, and F. T. Turner, Methane production and emission in a Texas rice field, *Global Biogeochem. Cycl.*, *4*, 47–68, 1990.

Sass, R. L., F. M. Fisher, P. A. Harcombe, and F. T. Turner, Mitigation of methane emissions from rice fields: Possible adverse effects of incorporated rice straw, *Global Biogeochem. Cycl.*, *5*, 275–287, 1991a.

Sass, R. L., F. M. Fisher, F. T. Turner, and M. F. Jund, Methane emission from rice fields as influenced by solar radiation, temperature and straw application, *Global Biogeochem. Cycl.*, *5*, 335–350, 1991b.

Sass, R. L., F. M. Fisher, Y. B. Wang, F. T. Turner, and M. F. Jund, Methane emission from rice fields: The effect of floodwater management, *Global Biogeochem. Cycl.*, *6*, 249–262, 1992.

Satpathy, S. N., A. K. Rath, B. Ramakrishan, V. R. Rao, T. K. Adhya, and N. Sethunathan, Diurnal variation in methane efflux at different growth stages of tropical rice, *Plant Soil*, *195*, 267–271, 1997.

Schütz, H., A. Holzapfel-Pschorn, R. Conrad, H. Rennenberg, and W. Seiler, A 3-year continuous record on the influence of daytime, season, and fertilizer treatement on methane emission rates from an Italian rice paddy, *J. Geophys. Res.*, *94*, 16,405–16,416, 1989a.

Schütz, H., W. Seiler, and R. Conrad, Processes involved in formation and emission of methane in rice paddies, *Biogeochemistry*, *7*, 33–53, 1989b.

Segers, R., and S. W. M. Kengen, Methane production as a function of anaerobic carbon mineralization: A process model, *Soil Biol. Biochem.*, *30*, 1107–1117, 1998.

Segers, R., and P. A. Leffelaar, Modeling methane fluxes in wetlands with gas-transporting plants, 1, Single-root scale, *J. Geophys. Res.*, in press, 2001.

Setyanto, P., A. K. Makarim, A. M. Fagi, R. Wassmann, and L. V. Buendia, Crop management affecting methane emissions from irrigated and rainfed rice in Central Java (Indonesia), *Nutrient Cycl. Agroecosys.*, in press, 2000.

Sigren, L. K., G. T. Byrd, F. M. Fisher, and R. L. Sass, Comparison of soil acetate concentrations and methane production, transport, and emission in two rice cultivars, *Global Biogeochem. Cycl.*, *11*, 1–14, 1997.

Singh, S., R. Batra, M. M. Mishra, K. K. Kapoor, and S. Goyal, Decomposition of paddy straw in soil and the effect of straw incorporation in the field on the yield of wheat, *Z. Pflanzenernähr. Bodenk.*, *155*, 307–311, 1992.

Slaton, N. A., C. A. Beyrouty, B. R. Wells, R. J. Norman, and E. E. Gbur, Root growth and distribution of two short-season rice genotypes, *Plant Soil*, *121*, 269–278, 1990.

Teo, Y. H., C. A. Beyrouty, R. J. Norman, and E. E. Gbur, Nutrient uptake relationship to root characteristics of rice, *Plant Soil*, *171*, 297–302, 1995.

Tsutsuki, K., and F. N. Ponnamperuma, Behavior of anaerobic decomposition products in submerged soils: Effects of organic material amendment, soil properties, and temperature, *Soil Sci. Plant Nutrient*, *33*, 13–33, 1987.

Turner, N. C., Crop water deficits: a decade of progress, *Adv. Agron.*, *39*, 1–51, 1986.

Tyler, S. C., R. S. Bilek, R. L. Sass, and F. M. Fisher, Methane oxidation and pathways of production in a Texas paddy field deduced from measurements of flux, $\delta^{13}C$ and δD of CH_4, *Global Biogeochem. Cycles*, *11*, 323–348, 1997.

van Bodegom, P. M., and A. J. M. Stams, Effects of alternative electron acceptors and temperature on methanogenesis in rice paddy soils, *Chemosphere*, *39*, 167–182, 1999.

van Bodegom, P. M., P. A. Leffelaar, A. J. M. Stams, and R. Wassmann, Modelling methane emissions from rice paddies: Variability, uncertainty and sensitivity analysis of processes involved, *Nutrient Cycl. Agroecosys.*, in press, 2000.

Walter, B. P., M. Heimann, R. D. Shannon, and J. R. White, A process-based model to derive methane emissions from natural wetlands, *Geophys. Res. Lett.*, *23*, 3731–3734, 1996.

Wang, B., H. U. Neue, and H. P. Samonte, Effect of cultivar difference ('IR72', 'IR65598' and 'Dular') on methane emission, *Agric. Ecosys. Environ.*, *62*, 31–40, 1997.

Wang, M.-X., A. G. Dai, J. Huang, L. Ren, W. Seiler, H. Schütz, H. Rennenberg, R. A. Rasmussen, and M. A. K. Khalil, Sources of methane in China: Rice fields, cattle, coal mining, sewage treatment, other minor sources, paper presented at CH_4 and N_2O Workshop: CH_4 and N_2O Emission From Natural and Anthropogenic Sources and Their Reduction Research Plan, Nat. Inst. of Agro-environmental Sci., Tsukuba, Japan, 1992.

Wang, Z. P., R. D. Delaune, P. H. Masscheleyn, and W. H. Patrick Jr., Soil redox and pH effects on methane production in a flooded rice soil, *Soil Sci. Soc. Am. J.*, *57*, 382–385, 1993.

Wang, Z. Y., Y. C. Xu, Z. Li, Y. X. Guo, R. Wassmann, U. Neue, R. S. Lantin, L. V. Buendia, Y. P. Ding, and Z. Z. Wang, Methane emission from irrigated rice fields in Northen China (Beijing), *Nutrient Cycl. Agroecosys.*, in press, 2000.

Wassmann, R., et al., Temporal patterns of methane emissions from wetland rice fields treated by different modes of N application, *J. Geophys. Res.*, *99*, 16,457–16,462, 1994.

Wassmann, R., H. U. Neue, M. C. R. Alberto, R. S. Lantin, C. Bueno, D. Llenaresas, J. R. M. Arah, H. Papen, W. Seiler, and H. Rennenberg, Fluxes and pools of methane in wetlands rice soils with varying organic inputs, *Env. Monitoring Assessment*, *42*, 163–173, 1996.

Watanabe, A., and M. Kimura, Methane production and its fate in paddy fields, VIII, Seasonal variations in the amount of methane retained in soil, *Soil Sci. Plant Nutrient*, *41*, 225–233, 1995.

Watanabe, A., K. Katoh, and M. Kimura, Effects of rice straw application on CH_4 emission from paddy fields, III, Effect of incorporation site of rice straw on CH_4 emission rates and their variation among shoots of a rice plant, *Soil Sci. Plant Nutrient*, *40*, 497–504, 1994.

Watanabe, A., M. Kajiwara, T. Tashiro, and M. Kimura, Influence of rice cultivar on methane emission from paddy fields, *Plant Soil, 176*, 51–56, 1995.

Watanabe, A., M. Yoshida, and M. Kimura, Contribution of rice straw carbon to CH_4 emission from rice paddies using ^{13}C-enriched rice straw, *J. Geophys. Res., 103*, 8237–8242, 1998.

Watanabe, I., Decomposition of organic matter in flooded rice soils, in *Organic Matter and Rice*, pp. 238–257, Int. Rice Res. Inst., Makati City, Phillipines, 1984.

Westermann, P., and B. K. Ahring, Dynamics of methane production, sulfate reduction and denitrification in a permanently waterlogged alder swamp, *Appl. Env. Microbiol., 53*, 2554–2559, 1987.

Yang, H. S., Modelling organic matter mineralization and exploring options for organic matter management in arable farming in Northern China, Ph.D. thesis, Wageningen Agric. Univ., Wageningen, 1996.

T. M. Metra-Corton, Agronomy, Soils and Plant Physiology Division, Philippine Rice Research Institute, Muñoz, 3119 Nueva Ecija, Philippines.

P. M. van Bodegom, Laboratory of Microbiology, Wageningen University and Research Center (WUR), H. van Suchtelenweg 4, 6703 CT Wageningen, The Netherlands. (bodegom@bio.vu.nl)

R. Wassmann, Soil and Water Sciences Division, International Rice Research Institute, Los Baños, Philippines.

(Received September 13, 1999; revised April 15, 2000;
accepted April 28, 2000.)